MACROEVOLUTIONARY PATTERNS IN THE NEW ZEALAND CENOZOIC TURRITELLID GENERA *ZEACOLPUS* AND *STIRACOLPUS* (GASTROPODA: TURRITELLIDAE)

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Ursula Erica Smith Ph. D.

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Gastropods have traditionally been extremely hard to construct phylogenetic relationships for because of the lack of easily coded morphological characters in their hard-parts. Many gastropod groups, such as the turritellids, are widespread and abundant in both the Recent and the fossil record, and other than the lack of available phylogenies are excellent candidates for addressing a wide variety of macroevolutionary questions, such as how new species occur. Here a new methodology for generating phylogenies for gastropods and other groups that have traditionally suffered the same problems is developed and applied.

New algorithms implemented in the phylogenetic analysis software Tree Analysis using new Technology (TNT; Goloboff et al., 2006) allows the inclusion of continuous data directly into an analysis rather than requiring arbitrary gap coding to reduce the continuous character data to discrete character states. This method uses TNT's ability to analyze continuous characters to allow detailed descriptions of shell shape to be incorporated and analyzed as continuous characters generated from a geometric morphometric (GM) shape analysis. A test case for the methodology using Recent members of the hyper-diverse genus *Conus*, which has an exceptional

molecular phylogeny, shows that GM-continuous characters generated from an eigenshape analysis can contribute to a phylogenetic hypothesis and allow the correct placement of taxa (such as fossils) that have only morphological data into a larger phylogenetic context.

A phylogenetic analysis of the two New Zealand turritellid genera *Stiracolpus* and *Zeacolpus* carried out using suites of GM-continuous characters generated from whorl profile shape and traditional discrete characters has generated the first phylogenetic hypothesis of turritellid gastropods. These phylogenies indicate that species of both genera have significant ghost ranges. When these ghost ranges are taken into account, the pattern of species originations appears very different from the raw appearance data through the New Zealand Cenozoic, with speciation events clustering in four stages rather than occurring gradually. Paleoenvironmental data suggests that species of the two genera had different environmental tolerances, with *Zeacolpus* being less well able to survive in the cooler conditions that *Stiracolpus* appears to have thrived in during the Pliocene to Recent.

BIOGRAPHICAL SKETCH

Ursula was born on the North Downs, in Surrey, England in September 1979. She attended Essendene Lodge Primary School, and completed her secondary education at Croydon High School. She took nine GCSEs in 1995 and then went on to study biology, chemistry, geography and mathematics at A-level which she completed in 1997.

In 1998, after taking a gap year and working for a year in industry, Ursula matriculated at New Hall, Cambridge University where she read Natural Sciences, specialising in Geological Sciences. She graduated in 2002 with a BA and an MSci. It was during her MSci project, investigating predation on gastropod mollusks in the Coralline and Red Crag deposits of East Anglia with Dr. Elizabeth Harper, that she became fascinated by snails.

Realizing a good palaeontologist should have a background in more than just geology, Ursula then applied for masters programs in biological sciences. She moved to Imperial College, London to study for an MSc, where she completed a project supervised by Drs. Jonathan Todd and Norman MacLeod of the Natural History Museum's Palaeontology Department applying geometric morphometric methods to species delimitation and identification in turrid gastropods. She graduated in 2003 and worked at the Natural History Museum as a Research Assistant for a year while applying to PhD programs.

Having spent her entire life living on chalk, Ursula moved to the Devonian shale of Ithaca in 2004 to pursue a PhD at Cornell University.

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During my time at Cornell I have been supported by the Department of Earth and Atmospheric Sciences by fellowships and teaching assistantships and by PRI as research assistantships, (which has been partly funded by National Science Foundation Grant EAR0719642). I have also been fortunate to have received financial support for travel to conferences from the Cornell Graduate School, the Department of Earth and Atmospheric Sciences Kauffman Grant and the Paleontological Research Institution (PRI).

The program TNT is made freely available, thanks to a subsidy from the Willi Hennig Society. The tps suite of program is made freely available by their author, F. James Rohlf. The Morpho-Tools notebooks for Mathematica are provided free of charge by their author Jonathan Krieger who has been very gracious in providing assistance with troubleshooting and updated code at intervals. Matthew Weyland wrote all of the IDL code used here.

An enormous number of people have contributed to the production of this dissertation, and I suspect I could write a dissertation of thanks alone. First and foremost, though, I must thank the members of my committee, Warren Allmon, John Cisne, Jeff Doyle and Amy McCune deserve huge thanks. I have learned much from each of them and am very grateful for their time and knowledge. I need to extend special thanks to my committee chair, Warren Allmon, who has been an incredible adviser during my time at Cornell. He has been excited about (even when I wasn't) and supportive of my work and has always found the time to mentor me despite his insanely busy schedule. I am incredibly grateful to him for everything he's done for me and helped me achieve while I've been at Cornell

While the majority of this work was carried out in Ithaca at Cornell EAS and PRI the GNS and The Monash Centre for Electron Microscopy at Monash University, Australia also provided me with space to work during extended visits at various points. I am grateful for all this institutions for allowing me space to work. I have been able to access material from a number of collections around the world and I would like also to extend thanks to the Collections staff at these institutions, particularly John Simes, Heidi Schlumpf and Craig Jones at GNS and Bruce Marshall at Te Papa Tongawera, The National Museum in Wellington, but also Neville Hudson at Auckland University Geology Department, Ewan Fordyce at Otago University Museum of Geology, Norton Hiller at Canterbury Museum, Wilma Blom and Margaret Morley at Auckland War Memorial Museum, Tom Darragh and Chris Rowley at Melbourne Museum and John Slapcinsky of the Division of Invertebrate Zoology, Florida Museum of Natural History; and Christina Piotrowski and Robert Van Syoc of the Invertebrate Zoology Section, the California Academy of Sciences.

In addition to working with museum collections, I've had the opportunity to spend some time in the field collecting, and for this, thanks need to be extended to Bruce Hayward of Geomarine Research and particularly to Bruce Maxwell. I had a wonderful time exploring the Eocene to Miocene outcrops of the Canterbury and Otago Basin with Bruce and was very much looking forward to our planned second trip the following year but unfortunately, Bruce died shortly before we were due to return to the field. He was incredibly giving of his time and expertise to a young graduate student with no real idea what she'd got herself into yet and his death was an enormous loss to the entire New Zealand palaeontology community.

James Crampton and Alan Beu of GNS have been enormously helpful, right from the very beginning of my research, providing copies of rare literature and pointing me in the right direction in the library at the start. They have both been giving of their time expertise and good humour and it isn't an exaggeration to say that my dissertation would not have happened without them. Austin Hendy has also been exceedingly helpful in fielding odd questions and discussing various New Zealand Cenozoic topics with me.

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teacher, Christine Muller, who first taught me about speciation many years ago. I'm sure neither of us knew where that initial introduction would take me, but I hope she'd be pleased.

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Jonathan Hendricks very kindly provided me with the aligned sequence data used in chapter one that allowed me to develop and test my methods and helped with taxonomic identification, photography and much discussion throughout. Beyond the

science, though, he has also been incredibly supportive and encouraging throughout my time as a graduate student even though we only overlapped at Cornell by one year. He has been an inspiration and a beacon of hope for life after graduate school.

My other palaeosibling, Mary Kosloski is also deserving of special mention. She has been a constant source of amusement, support and inspiration in all aspects of life since her arrival in Ithaca, from reading and commenting on multiple drafts of my dissertation to the almost equally important provision of chocolate and laughter over the years. We've mooched around Ithaca together and traveled the country together and I shall miss sharing an office with her immensely.

Finally, but not in anyway least, my family deserve recognition for everything they've done for me over the years, not least putting up with my being several time zones away from them for an extended period. Matt has been a source of constant support and understanding despite being on the other side of the world for the last three years and I'm looking forward now to being able to actually spend time with him. Without the love and the encouragement of my parents, Angela and Geoff, and also my brother, Ian, I would certainly not be writing this acknowledgements section today. My parents gave me a love of learning and of science as a child and instilled in me a belief that I could do anything I wanted to when I grew up. I'm not sure that they envisioned that leading to a PhD in palaeontology from an institution on the other side of the Atlantic, but despite their consternation, they continued to be nothing but supportive when I made the move to Ithaca. I am more grateful to them than I can express for everything.

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CHAPTER 1

GEOMETRIC MORPHOMETRIC CHARACTER SUITES AS PHYLOGENETIC DATA: EXTRACTING PHYLOGENETIC SIGNAL FROM GASTROPOD SHELLS

Abstract

Gastropods are one of many taxa for which morphological phylogenies have been difficult to construct, particularly for fossil taxa, due to a lack of available discrete characters in their mineralized hard parts. The introduction of methodologies for including continuous data directly in a phylogenetic analysis is increasing the number of available characters, making it possible to produce phylogenies for these taxa. Geometric morphometric methods provide tools for accurately describing shape variation and can produce continuous data that may be included in a phylogenetic matrix. Here, the hyperdiverse marine gastropod genus *Conus* is used to evaluate the ability of continuous characters generated from a geometric morphometric analysis to contribute to a phylogenetic hypothesis in combination with other data sources (here nuclear and mitochondrial genetic sequence data) by comparing molecular and total evidence phylogenies. Additionally the ability of continuous characters derived from geometric morphometrics analyses to place fossil taxa with limited characters into a phylogeny with their modern relatives was tested by simulating the inclusion of fossils. This was done by removing the molecular partition of individual modern species to produce a "cladistic pseudofossil" with only geometric morphometric derived characters and comparing the position of the cladistic pseudofossil taxon in a phylogeny with its placement in the total evidence tree. In over half of the test cases, it was possible to successfully place a species lacking molecular data into the

phylogeny using only continuous characters generated from geometric morphometric data. This suggests that the incorporation of fossils into modern phylogenies will be possible for *Conus*, opening up a wide range of macroevolutionary questions to study with this genus. This methodology also has potential to contribute to phylogenetic reconstructions for other taxa that have traditionally had few discrete morphological characters such as other gastropod groups, but also other phyla.

Introduction

A phylogenetic framework is essential in order to address a wide variety of evolutionary problems such as examining species selection or modes of speciation (e.g., see Cooper and Fortey, 1998; MacLeod, 2001a). It is often desirable to incorporate fossils into macroevolutionary studies using extant species, not just to investigate the relationships of ancient to their Recent relatives. Fossils can provide information not just about the timing of events in the group's history, but also information about the sequence of character evolution within a group as well as providing information about unique morphologies that may no longer be represented in extant species (see Hermsen and Hendricks, 2008 for an overview).

Molecular sequencing efforts are increasing the quantity and quality of molecular data available for many groups. While useful for producing robust phylogenies for modern representatives of a clade, however, there are a great number of extant taxa, as well as the more obvious fossil taxa, for which molecular data are not currently, and will never be, available (Donoghue et al., 1989; Smith and Turner, 2005), making it impossible to examine the relationships of fossil species or to place fossils into the

phylogenetic context of their modern relatives. To include these taxa into an analysis, therefore, other sources of character data must be utilized.

As a general rule, the number of characters required to generate a robust and well resolved phylogeny in a phylogenetic analysis is approximately twice the number of taxa in the matrix or at the least, *n*-1 synapomorphies for *n* taxa (Eldredge and Cracraft, 1980). Therefore, the number of morphological characters required for a purely morphology-based analysis for a large number of taxa far outstrips the number of morphological characters that are generally described in many invertebrate taxa, particularly in the case of fossils where only mineralized hard parts are available such as bivalves, cephalopods or corals.

Taxa that have the most potential for macroevolutionary studies are those with the richest fossil histories because of their mineralized hard parts. However, these are (with the notable exception of echinoderms and arthropods), generally groups in which the most abundant and most phylogenetically useful characters occur in the non-mineralized, and therefore rarely preserved, soft-part anatomy. In the case of mollusks the shell is, with some rare exceptions, the only portion of the organism preserved in the fossil record, meaning that the shell is all that is available from which to gather phylogenetic characters; a task that has proved difficult in past analyses.

To compound this problem, where hard parts are preserved, it has often proved extremely difficult to reduce the continuous variation of hard part morphology into discrete characters for phylogenetic analysis. However, with the advent of new computational techniques for directly analyzing continuous character data in phylogenetic analysis (e.g., Goloboff et al., 2006), it is now becoming possible to

incorporate continuous characters. While most studies utilizing this technique have been applied to taxa that have traditionally not been as character poor as gastropods, there have been some promising results (e.g., Goloboff et al., 2006; González-José et al., 2008; Mirande, 2009; Poore, 2009).

The utility of continuous characters

The use of shell morphology in phylogenetic analysis of Recent or fossil gastropods does assume that shell morphology is a reliable indicator of both taxonomic identity and phylogenetic relationships and is not rife with homoplasy (i.e., similarity due to convergence rather than common ancestry), a point that has been debated (e.g., Kool, 1993; Emberton, 1995; Schander and Sundberg, 2001; Wagner, 2001). All extinct, and the vast majority of extant gastropod taxa, were originally described on the basis of their shell features, with soft part anatomical features being incorporated more recently in descriptions of extant species. In the case of gastropod mollusks, there is clearly systematic variation in shell morphology that allows species to be recognized, and in describing this interspecific variation, morphometric variables are often used, even if these are simply length measurements such as widths and heights rather than being formalized via morphometric methodologies (e.g., Cole et al., 2002; Polly, 2002).

While this species level taxonomic variation must have a phylogenetic basis (Forey, 2002), it has been largely underutilized in phylogenetic analyses due in part to the belief that gastropod shells do not contain a phylogenetically useful signal. It has been widely held that homoplasy renders shell characters useless (e.g., Kool, 1993) both because their morphology is plastic in response to environmental factors and because,

as protective structures, they are targets of intense selection pressure. Some recent studies have shown, however, that shell characters are perhaps not as problematic as had previously been thought (e.g., Schander and Sundberg, 2001) and many workers now accept that morphological characters should not be rejected *a priori*. Indeed, there have been phylogenetic studies carried out that utilize only shell characters (e.g., Wagner, 1999). In addition, other studies have shown that while shell characters are more homoplasious than anatomical or molecular characters, they can contribute to phylogenetic hypotheses as components of combined analyses, adding resolution and increased node support within the phylogeny (e.g., Vermeij and Carlson, 2000; Wagner, 2001; Collin, 2003). In this way, shell characters appear able to add resolution to a phylogenetic hypothesis and increase node support within the phylogeny. This is consistent with studies in other phyla using morphological data combined with molecular data (e.g., Hermsen and Hendricks, 2008).

However, beyond the problem of the homoplasy of shell characters, there has also been great difficulty in defining potentially homologous characteristics between gastropod shells and partly due to the difficulty encountered in describing the complex and continuous variation as discrete characters. This problem is not restricted to gastropods and other mollusks and the topic of how continuous characters should be coded and incorporated into phylogenetic analyses has been hotly debated. While it has been argued that continuous data should be excluded from phylogenetic analyses (e.g., Pimental and Riggins, 1987; Cranston and Humphries, 1988; Felsenstein, 1988; Bookstein, 1994; David and Laurin, 1996), a vocal group has argued since the early 1990s for the inclusion of all available data, including continuous data (e.g., Stevens, 1991; Thiele, 1993; Rae, 1998).

The comparability of qualitative and quantitative data is now widely accepted as recent studies have demonstrated that continuous data described by general morphometric methods are suitable for inclusion in phylogenetic analyses (e.g., Rae, 1997, Rae, 1998; Swiderski et al., 1998; Zelditch et al., 2000; Zelditch et al., 2001; Felsenstein, 2002; Humphries, 2002; Rae, 2002; Jensen, 2003). As Zelditch et al., (2001) succinctly point out "some objections ostensibly directed at quantified shape data apply equally well to all shape data, or perhaps even to all data, not quantified size and shape data exclusively". However, even amongst those who agree that continuous data should be included in a phylogenetic analysis, little consensus has been achieved on *how* such data should be used in a phylogenetic context.

As Felsenstein (2002) points out, much of the problem associated with utilizing continuous characters has been the requirement of available analysis software for discrete character states. A large part of the ongoing debate about how to use continuous characters has therefore been the ongoing discussion of how to code continuous characters in general into discrete character states for analysis (e.g., Almeida and Bisby, 1984; Thorpe, 1984; Archie, 1985; Baum, 1988; Goldman, 1988; Chappill, 1989; Thiele, 1993; Strait et al., 1996; Stevens, 2000; Wiens, 2000b; Wiens, 2001; Reid and Sidwell, 2002; Guerrero et al., 2003; Garcia-Cruz and Sosa, 2006), but there has also been some discussion about alternative methods of using continuous characters (e.g., Lee et al., 2006; Thuillard and Fraix-Burnet, 2009).

The software TNT (Tree analysis using New Technology; Goloboff et al., 2006; Goloboff et al., 2008), now allows the direct analysis of continuous characters without requiring that they be broken down into discrete states. While this does not address the underlying issue of whether or not continuous characters are suitable for use in

phylogenetic reconstruction it has opened up new possibilities for the use of morphometric data in phylogenetic inference and made much of the debate regarding how to code continuous characters less relevant than during the peak of the morphometric/phylogenetic coding debate (e.g., Wiens, 2000a; Adrain et al., 2001; MacLeod and Forey, 2002). A number of studies have now begun to incorporate continuous data into phylogenetic analyses using TNT's ability to analyse continuous data (e.g., Domínguez and Roig-Juñent, 2008; González-José et al., 2008; Hornung-Leoni and Sosa, 2008; Hendrixson and Bond, 2009; Mirande, 2009; Poore, 2009; Vega et al., 2009).

Geometric Morphometrics

Traditional morphometric methods refer to basic measurements of length such as widths and heights which have been, and still are, widely used to describe and compare shape to address a variety of questions through the phyla. Examples applying traditional morphometrics to gastropods include quantifying shape variation between species and identifying Raupian parameters (e.g., Kohn and Riggs, 1975), examining morphological variation in systematic studies (e.g., Allmon, 1996) or studying intraspecific variation (e.g., Janson and Sundberg, 1983). However, length measurements are limited in the shape information they can capture about an organism and do not always distinguish between size and shape variation (e.g., see Zelditch et al., 2004). To address this problem, geometric morphometric techniques were developed (see Adams et al., 2004 and Lawing and Polly, 2010 for discussion of the history of geometric morphometrics) that analyze the geometry of the shape in question and therefore retain more information about shape variation. Initially these methods used sets of landmarks positioned on points assumed to be homologous

which were then analyzed using relative warps analysis (analogous to principle component analysis of length data).

More recently, techniques in biology for the analysis of curves have been developed, such as eigenshape analysis (MacLeod, 1999) and Fourier analysis (Foote, 1989; Crampton, 1995, Haines and Crampton, 2000). Rather than using discrete points that are assumed to be homologous, as with the end points of traditional measurements or landmark analyses, these techniques define shapes using a large number of "semi-landmarks" (x-y coordinate points that are not assumed to be homologous but are used to define the shape only). The use of semi-landmarks rather than discrete homologous points, allows comparison between shapes which might not necessarily contain the same set of homologous discrete landmark points.

Geometric morphometric methods have enjoyed an enormous surge in popularity since the "morphometric synthesis" (Bookstein, 1996; see also Jensen, 2003 and Adams et al., 2004 for summaries) and are now regularly applied to the analysis of shape variation in a wide range of taxonomic groups. These studies not only utilize size data from centroids calculated using landmarks (eg., Lockwood, 2005; Wood et al., 2007), but also actively examine shape for reasons as diverse as quantifying differences in shape disparity between groups (eg., Marugán-Lobón and Buscalioni, 2004), or within groups (e.g., Vidal et al., 2005), looking at links between morphology and diversity (e.g., Lockwood, 2004) and taxonomy (e.g., Douglas et al., 2001; Baylac et al., 2003; Guy et al., 2003; Becerra and Valdecasas, 2004), examining deformation in fossils (Angielczyk and Sheets, 2007) and reconstructing paleoclimate from leaf shapes (Krieger et al., 2007). Morphometric methods are even being applied in quantitative genetic studies, (e.g., Klingenberg and Leamy, 2001; Klingenberg et al.,

2001). Studies applying non-traditional morphometric methods to mollusks include using Fourier transformations and Geographic Information Systems to examine ammonoid suture shape (e.g., Manship, 2004; Allen, 2006) and many studies of size and shape in bivalves (e.g., Crampton, 1995; Costa et al., 2008; Innes and Bates, 1999). Several studies have also now applied geometric morphometric methods to gastropods, (e.g., Guralnick and Kurpius, 2001; Teusch and Guralnick, 2003; Rolán et al., 2004; Carvajal-Rodríguez et al., 2005; Hollander et al., 2006; Conde-Padín et al., 2007; Cunha et al., 2008; Monnet et al., 2009).

Despite the increasing number of studies applying geometric morphometric methods to mollusks, a perceived obstacle in their application to gastropod shells (and other structures that exhibit accretionary growth), has been the difficulty of defining homologous points between taxa, a problem now reduced by the development of semi-landmark methods. However, while also relevant in traditional morphometric studies, homology is often ignored and measurements use end points that are implicitly assumed to be homologous though often are not (e.g., Estebenet and Martín, 2003; Olabarria and Thurston, 2004; Anderson et al., 2007; Preston and Roberts, 2007). The measurements used in such studies to examine size or shape are generally arbitrary points such as those corresponding to a shell's widest or tallest point, but that are not necessarily homologous between specimens or species. For example, some gastropod taxa have shells that are widest at the shoulder, while closely related species are wider below the shoulder but the differing location of the widest point on the shell is not taken into account when being measured.

As homology between semi-landmarks is not assumed, semi-landmark based methods such as eigenshape analysis appear ideal for use with groups such as the gastropods

where defining homologous points between species has proved so difficult. Such semi-landmark based methods, are starting to be applied to the shells of gastropods (e.g., Teusch and Guralnick, 2003). For example, in the case of *Conus*, by using the outline of the entire shell as described in this method (see figure 1.1), it is possible to incorporate nearly all of the linear components of shape described by Kohn and Riggs, 1975, figure 1.3) in a single outline.

Using geometric morphometric methods to generate phylogenetic characters

Beyond the discussion about the use of continuous data in phylogenetic analysis, there has also been much debate focused on the fundamental suitability of geometric morphometric methodologies for the description and coding of those continuous variables. Some studies have attempted to use morphometric methods directly to derive new phylogenetic characters (e.g., Swiderski, 1993; Zelditch et al., 1995; MacLeod, 2002; Bookstein, 2002). Others argue that use of morphometrics should be limited to enhancing descriptions to produce more accurate traditional phylogenetic characters rather than in generating new morphological characters (e.g., Zelditch et al., 2001).

Most geometric morphometric methods are eigenanalysis-based (e.g., principal components analysis, relative warps analysis, eigenshape analysis), meaning that the dataset undergoes a decomposition which generates a new set of axes along which shape is partitioned as independent components of the shape variation in the original

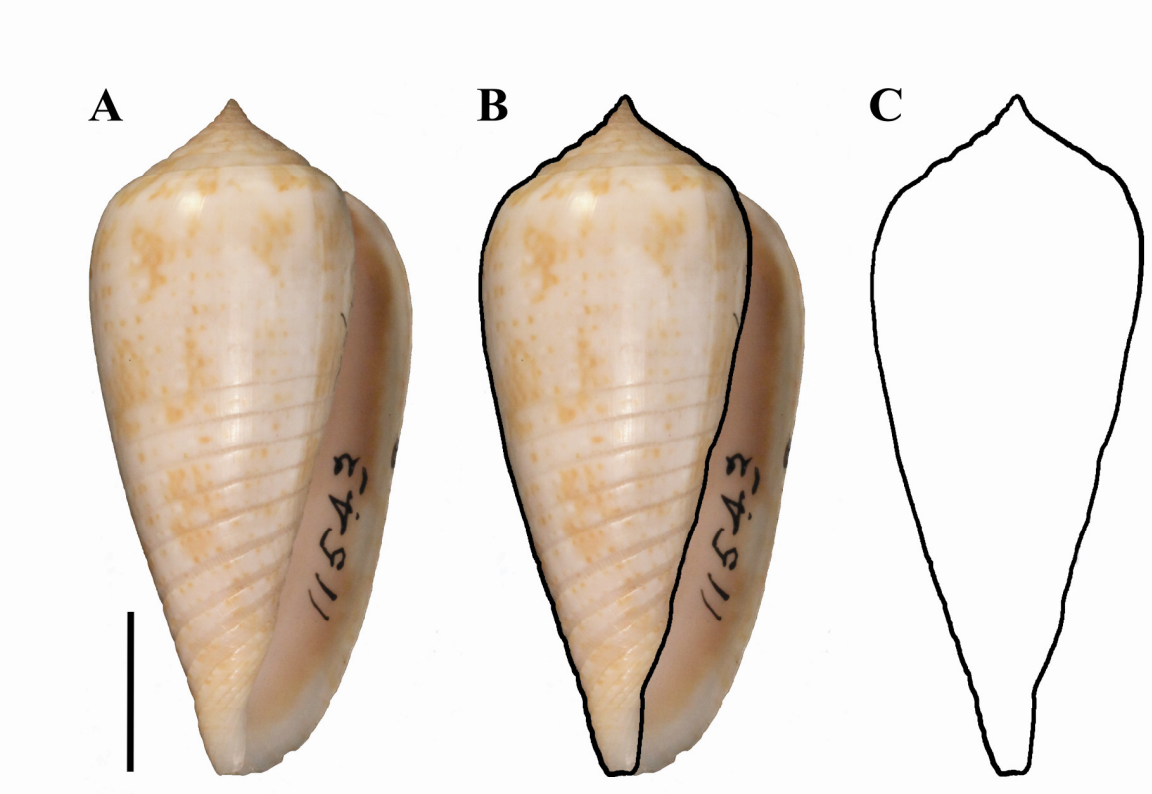

Figure 1.1: A: Raw image of *Conus cinereus* (CAS180459). B: Outline traced around spire and body whorl. C: Outline that is then converted to coordinates using tpsDig. Thickness of trace line is for illustrative purposes only. A real outline used in an analysis as described here would be much finer in order to capture more detail of the shell outline.dataset. Each eigenaxis produced by this decomposition accounts for a certain proportion of the shape variation in the dataset. For instance, the first axis, describing the most variation in the dataset, may show change in size, while the second may show a change in the angle of a structure. Adding all of the axes back together describes the total shape variation in the dataset. The position of a specimen along an axis (given by its eigenscore or eigenaxis loading) indicates where it lies in the spectrum of shape variation described by that axis, see figure 1.2. As each axis describes a different component of shape variation, taking the position of a specimen on every axis in the dataset allows its complete shape to be reconstructed. Every species occupies a range of shape space along each axis and therefore intraspecific shape variation can be described.

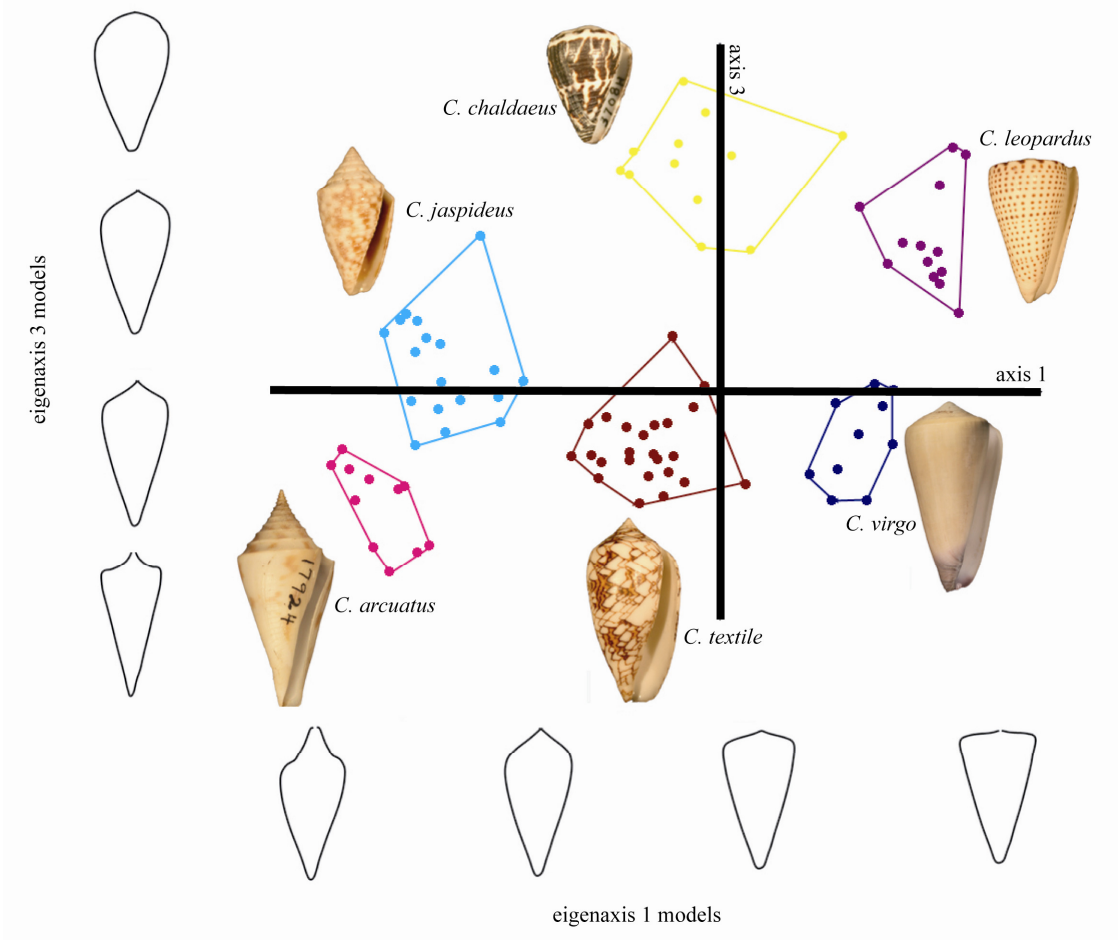

Figure 1.2: Example showing how shape varies along two eigenaxes. The eigenaxis models show generalizations of how shape varies along each eigenaxis. Here, eigenaxis 1 shows variation from high-spired shells at low values to low-spired shells at higher values while eigenshape 3 shows variation from concave spire shape at low values to convex spires at higher values. The position of each of the 5 species shown here is indicated by their positions along each axis. For instance, *C. arcuatus* has low scores on both eigenaxes as it has a high, concave spire. Moving up eigenaxis 3, *C. jaspideus* has a more concave spire, but is still high-spired. Moving along eigenaxis 1 from *C. arcuatus*, *C. textile* has a lower spire which is still quite concave. *C. leopardus*, the species with the highest score on eigenaxis 1, has the flattest spire in this example.

It has been argued that data from any eigenanalysis-based methodologies should not be used in the definition of phylogenetic characters because the results of the analysis are based upon the composition of the sample used such that adding another specimen will change the shape space generated by the eigenanalysis (e.g., Rae, 2002; Swiderski et al., 2002; Zelditch et al., 2004) as this would break the criterion of phylogenetically useful characters being features of individual organisms (Pimental and Riggins, 1987) despite genera often being unhesitatingly coded as terminal taxa. MacLeod (2001b, 2002) argues that morphometric-based methods producing sample-referenced results should not be excluded from use in phylogenetic inference as all phylogenetic characters are defined with reference to the sample (e.g., something "complex" in one sample set could be considered "simple" in another) and that therefore, with care not to use a dataset that alters significantly with the removal or addition of specimens, such data can be incorporated into a phylogenetic analysis.

A number of methods have previously utilized ordination data in defining characters and character states, for instance, a form of gap coding has been suggested (MacLeod, 2002) which uses discontinuities in continuous data by assigning character states to groupings in the shape space produced by an eigenanalysis decomposition. This approach can be problematic if no obvious groupings are uncovered, or if arbitrary groupings are picked out of the plots (in the same way as arbitrary groupings can be picked by other gap coding methods, e.g., Reid and Sidwell, 2002). However, MacLeod's example using trilobites and simulated fish showed that that this approach is able to recreate phylogenies based on other data sets even if some data is lost in the conversion from continuous variables to discrete characters (Adams et al., 2004).

The method described in this paper extends the use of the position of specimens and species in shape space as described by eigenaxis loadings. Rather than discretely coding a species along an axis based on possibly arbitrary groupings, each species' position along each axis is included directly into the analysis as continuous characters from the eigenscores produced by the eigenshape analysis. As described above, the position of a specimen (or species) along each axis indicates what the original shape of that specimen was. To incorporate the shape of a specimen or a species into a phylogenetic analysis the coordinates describing its location along each eigenaxis (i.e. its eigenscores) can therefore be incorporated directly into TNT as continuous characters.

Zelditch et al. (2001) argue against the use of principle components scores (and as an extension, therefore, relative warp scores and eigenscores) as they are descriptions of what might be homologous features rather than the axes generated being homologous in their own right. However, though individual axes are just geometrically independent descriptions of shape variation, as described above, the combination of all the ordination axes represents the total shape variation in the sample and therefore using multiple ordination axes in a phylogenetic analysis, allows an integrated complex phenotype to be treated as a single homologous phylogenetic unit and analyzed as a whole structure rather than as a series of univariate characters (see González-José et al., 2008).

A shell is a complex structure that may be analyzed in this manner. As gastropod shells are assumed to be homologous across the class the shape of the shell, is homologous between them. As described above, defining homologous points on gastropod shells has been problematic, but the use of semi-landmarks and eigenshape

analysis allows the entire homologous structure to be described and avoids the problem of locating strictly homologous points within that structure. This therefore allows the shape of the shell to be incorporated into a phylogenetic analysis.

In their 2008 phylogenetic study of *Homo* fossils, González-José et al., used a similar methodology to that described here, but used relative warp scores from a 3D landmark analysis rather than eigenshape analysis as landmarks are more easily identified on *Homo* skulls. Using the relative warp scores for individual specimens (whereas here the standard error around the mean value of each species is used), they found that using only the relative warp scores and no other characters recovered a phylogeny showing a marked congruence with other, independently generated, phylogenies. However, their reference phylogeny was also based on morphological characters and may therefore not be a completely independent case (Hendrixson and Bond, 2009).

A test case for continuous characters: The hyperdiverse marine gastropod genus Conus

To address the question of whether or not continuous shell character data contain a phylogenetic signal, it is necessary to have an independent reference phylogeny with which to compare (Hendrixson and Bond, 2009). As many invertebrate groups are limited, even with modern species, to phylogenies based on morphology alone, this can be very difficult. The hyperdiverse (more than 500 extant species; Röckel et al., 1995) marine gastropod genus *Conus* therefore makes an ideal test group as there is abundant molecular sequence data of modern species available to generate reference molecular phylogenies. It also has a rich and diverse fossil record making it possible to address a variety of interesting macroevolutionary questions.

There have been a paucity of described shell characters described in *Conus* (e.g., Rolán, 1992; Röckel et al., 1995; Duda et al., 2001) and Hendricks (2005) was able to use only 16 shell characters in a combined morphological and molecular study. Until the introduction of molecular phylogenetic techniques, therefore, the infrageneric relationships of *Conus* were poorly understood. With the advent of these methodologies a number of gene and conotoxin (neurotoxins produced by *Conus*) sequences have now been utilized in reconstructing species relationships within *Conus* (e.g., Duda and Palumbi, 1999; Conticello et al., 2001; Duda et al., 2001; Espiritu et al., 2001; Oliveira, 2002; Duda and Rolán, 2005; Duda and Kohn, 2005; Cunha et al., 2005; Cunha et al., 2008).

Only one study (Cunha et al., 2008) has thus far applied geometric morphometric methods in studying *Conus* shells and this used landmarks and semi-landmarks were used to explore shape variation in a clade of Cape Verde *Conus* in relation to taxonomy and geographic distribution. While the landmarks used may capture the shape variation in the species in the study, they will have limited utility outside their study clade as many of them are based upon the sutures between whorls, making them narrowly applicable as they assume the same number of whorls per species.

Some studies have suggested that the shell of *Conus* does not contain an unequivocally useful phylogenetic signal, for instance, Cunha et al., (2008) found their landmark morphometric analysis did not recover groupings consistent with the molecular phylogeny produced by analysis of two mitochondrial genes, despite their conclusion that "subtle shell shape features may have some discriminating utility for taxonomic purposes"). Other studies, however, have shown that the addition of morphological characters to the molecular data provides significant supplemental information that

leads to a greater resolution of the resulting phylogeny for parts of the *Conus* genus (Hendricks, 2005).

This study does not aim to use continuous characters alone to generate a phylogeny or provide new insights into the phylogeny of *Conus*. Rather, it aims to evaluate the utility of continuous characters generated from a geometric morphometric analysis for placing taxa that are missing molecular data into a phylogenetic framework. A total evidence approach (also known as combined analysis, simultaneous analysis and the supermatrix approach (Kluge, 1989; Nixon and Carpenter, 1996; de Queiroz and Gatesy, 2007)) was used to generate a phylogeny of extant taxa based on molecular and morphological characters as a reference. The potential for placement of fossil taxa in the resulting phylogeny was evaluated by simulating the inclusion of fossil taxa by removing molecular data from individual species in the total evidence matrix and comparing the resulting phylogenies from the total evidence matrix with those resulting from the individual matrices that included simulated fossils. This allowed the evaluation of how well fossil taxa could be placed into a phylogenetic analysis based on morphological data. While other morphological characters (e.g., color patterns or ornament) may be phylogenetically informative in *Conus* (e.g., see Hendricks, 2005) they were not used here in order to perform a more stringent test of the geometric morphometrics derived continuous characters.

Methods

The species used here were selected using the calmodulin phylogeny of Duda and Kohn's 2005 study (see Duda and Kohn, 2005, figure 2) for which 16s rRNA (e.g., Espiritu et al., 2001) and calmodulin intron molecular data (the most widely utilized

sequence data in previous phylogenetic analyses of *Conus* (e.g., Duda et al., 2001; Duda and Kohn, 2005)), are available. Sixty-one *Conus* species (see table 1.1 and appendix 1) represented by well-preserved museum samples were included. An effort was made to sample as widely as possible with the subclades of *Conus* recognized by Duda and Kohn (2005) while still using species for which both sets of molecular data were available as increased accuracy is obtained through increased taxon sampling (e.g., Pollock et al., 2002). The majority of specimens came from the Paleontological Research Institution and California Academy of Sciences, with some additional material from the malacology collections of the Florida Museum of Natural History (FLMNH) and the University of Kansas Division of Invertebrate Paleontology to increase sample sizes where initial numbers of available specimens were low.

There are no consistent rules for selecting specimen numbers for a morphometric analysis but larger sample sizes are obviously more desirable. Here, initially species were only included for study if more than 10 specimens were available. In the final dataset, some specimens were discarded leaving some species with fewer than 10 (e.g., n=9 see table 1.1) if it was determined that selected specimens were of dubious taxonomic affinity or the outline of the shell was obscured (e.g., by damage or by encrusting organisms).

Conus californicus was used as the outgroup as previous studies show that it is a sister taxon to the other species in this study (Duda et al., 2001; Espiritu et al., 2001; Duda and Kohn, 2005; Biggs et al., 2010). While one or more neogastropod taxa outside of *Conus* would ideally be used as outgroups, no appropriate taxa could be found in the NCBI database that possess both of the genetic regions possessed by all of the ingroup

Table 1.1: (Carries over next two pages) Species list showing specimen numbers and results of cladistic pseudofossil analyses. Values of 'b', 'x' and 'number of species missing from agreement tree' indicate how much disruption has occurred in the cladistic pseudofossil analysis (see text and figure 1.5 for explanation of these metrics). For original and new clade numbers, see figure 1.3. The CI and RI of all cladistic pseudofossil phylogenies are extremely similar to those of the total evidence phylogeny.

	Specimen Numbers														
	CAS	PRI	Florida	Kansas	Total	Success	bx=	x=	No. species missing from agreement tree	Topology altered elsewhere on phylogeny?	Original clade #	New clade #	Node support on Calmodulin phylogeny	CI	RI
abbreviatus		9		1	10	yes	2	6	1	no	56	50		0.291	0.442
anemone	10	5			15	no	3	11	4	no	24	43	no	0.292	0.446
araneosus	12	1			13	no	2	7	1	no	40	14		0.291	0.446
archon	8		3		11	no	3	16	6	yes	11	4	no	0.277	0.399
arcuatus	10				10	yes	1	4 &5	4	yes	2	3?	no	0.285	0.415
balteatus	7				7	no	3	13	3	no	24	34	no	0.288	0.436
bandanus	5	4			9	yes	0	0	0	no	41	x		0.290	0.442
brunneus	8	3			11	no	3	15	6	yes	12	34		0.288	0.432
californicus		14			14	-	-	-	-	-	-	-	-	-	-
catus		11			11	yes	5	5&8	2	no	54	48		0.288	0.433
chaldaeus		13			13	yes	1	1	1	no	59	58?		0.287	0.432
cinereus	5	6			11	no	3	10	4	no	29	44		0.287	0.438
coronatus		9			9	yes	0	0	0	no	57	x		0.288	0.432
dalli	6	4			10	no	2	9	2	no	43	29		0.287	0.433
daucus		8			8	no	4	10	5	yes	20	14		0.289	0.443
diadema	8	2			10	no	2	11	1	no	34	11		0.289	0.432
distans	4	6			10	no	5	18	15	yes	7	32	no	0.289	0.443
dorreensis	6	6			12	no	2	15	1	no	58	3		0.288	0.432
ebraeus		37			37	yes	1	1	1	no	59	58?		0.287	0.431
eburneus		19			19	yes	0	0	0	no	38	x		0.285	0.430
episcopatus	9	4			13	yes	1	1	1	no	45	44?		0.288	0.436
figulinus		8			8	no	2	7	5	yes	37	27	no	0.289	0.439
flavidus		6			6	no	2	12	2	no	32	6		0.287	0.436
furvus	11	5			16	no	2	7	1	no	29	14		0.290	0.439
generalis		6	4		10	no	2	6	3	no	14	11	no	0.288	0.439
geographus	5	7			12	no	2	5	5	yes	48	52		0.286	0.435
gladiator		12			12	no	2	7	1	no	21	10		0.285	0.427
imperialis		11			11	no	1	9	1	no	10	31	no	0.290	0.442
jaspideus		19			19	yes	1	1	1	no	3	2?		0.288	0.414
leopardus		13			13	no	2	10	2	no	31	10	no	0.288	0.439
lithoglyphus		5	6		11	no	2	10	3	yes	14	6	no	0.288	0.439

Table 1.1 Continued

	Specimen Numbers													
	CAS	PRI	Florida	Kansas	Total	Success	bx=	x=	No. species missing from agreement tree	Topology altered elsewhere on phylogeny?	Original clade #	New clade #	Node support on Calmodulin phylogeny	CI	RI
lividus		14			14	no	2	9	1	no	34	17		0.288	0.432
magus		20			20	no	2	10	1	no	54	29		0.287	0.433
mahogani		12			9	yes	1	1	1	no	5	4		0.286	0.409
marmoreus		12			12	yes	0	0	0	no	41	x		0.292	0.447
miles	10	18			28	no	2	10	1	no	18	34		0.286	0.429
miliaris		12			12	yes	0	0	0	no	56	x		0.289	0.436
mus		21			21	no	2	10	3	no	21	11		0.285	0.429
musicus	7	3			10	no	2	11	3	no	49	34		0.285	0.433
nux		7			7	yes	1	1	2	no	50	x		0.287	0.430
omaria		12			12	yes	1	1	1	no	44	44		0.288	0.436
patricius	2	7	4		13	no	3	9	3	no	23	37	no	0.290	0.442
pennaceus	4	8			12	yes	1	1	1	no	45	44		0.288	0.435
perplexus		18			18	no	2	9	1	no	4	11		0.285	0.414
planorbis		10			10	no	1	5	1	no	6	14		0.290	0.440
princeps		15			15	no	2	10	3	no	22	6	no	0.288	0.438
pulicarius		23			23	no	4	8	9	yes	27	38	no	0.286	0.438
purpurascens		12			12	yes	3	8	4	yes	26	33		0.289	0.441
quercinus		19			19	no	2	10	1	no	35	11		0.289	0.437
rattus	10	7			17	no	3	10	6	yes	17	34		0.287	0.432
regius	6	2			8	no	2	9	1	no	12	21		0.293	0.449
sponsalis		12			12	yes	2	6	1	no	50	56		0.285	0.431
stercusmuscarum	6	3	2		11	yes	1	1	1	no	52	53		0.287	0.435
striatus		24			24	yes	2	4	1	no	53	48		0.287	0.435
tessulatus		12			12	yes	0	0	0	no	38	x		0.285	0.431
textile		23			23	yes	1	1	1	no	43	42		0.286	0.433
tulipa	5	6			11	no	3	4	6	yes	48	48		0.289	0.436
varius	7	3			10	no	1	6	1	no	8	18	no	0.290	0.438
vexillum	8	5			13	no	2	6	1	no	18	8		0.286	0.431
virgo		10			10	no	3	9	2	no	32	14		0.288	0.435
ximenes		7			10	yes	1	2	1	no	5	4		0.286	0.408
				Total:	808										

taxa. An ideal outgroup candidate for exploring *Conus* phylogeny would be *Conorbis,* but material is very rare. While shells of *Conorbis* were located in the dry FLMNH collections it was represented by too few specimens (three) to be included in the geometric morphometrics analysis. Additionally, no molecular data are currently available for the genus and no wet collection material from which sequencing could be carried out has been located. For the rest of this paper, the generic abbreviation *C.* refers to *Conus*.

Molecular data

Calmodulin and 16S rRNA sequence data were downloaded from the National Center for Biotechnology Information's GenBank database (NCBI) (see appendix 2). Each region was individually aligned using the online software MUSCLE (ver. 3.7; Edgar, 2004). Alignment ambiguities discovered by repeat alignments using MUSCLE were then removed from each aligned sequence files using the software Gblocks (ver. 0.91; Castresana, 2000). The "Minimum length of a block" function was set to "5" and "the treatment of gaps" function set to "with half" (i.e., allowing gaps to persist if present in 50% of more of taxa; see Cartwright et al., 2008, who also utilized a similar protocol). Gblocks retained 407 (61%) of the 16s characters and 255 (39%) of the calmodulin characters. Both sets of sequence data were then combined into a single data matrix (hereafter called the molecular partition) using the software program WinClada (ver. 1.00.08; Nixon, 2002). The resulting molecular partition contained 662 DNA characters, though 387 of these were found to be uninformative and were deactivated during the phylogenetic analyses, leaving 275 informative DNA characters.

Morphological data

Digital images of each *Conus* specimen were taken in standardized apertural view such that the axis of coiling and opening of the aperture were parallel to the lens of the camera. In Photoshop (ver. 6.0; Adobe, 2000), all images were adjusted to the same scale and the outline of the spire and body whorl, excluding the aperture and apertural lip, (which are often, if not usually, broken) were digitized by tracing the shape of the outline using a digital tablet. This produced a closed outline trace, (figure 1.1), that was exported as jpeg image then converted to coordinate points using tpsdig (ver. 2.12; Rohlf, 2008). Outline coordinates were then reordered using code in IDL (ver. 5.6; ITT Visual Information Solutions, 2002) so that the starting point of each outline corresponded to the apex of the spire, the only easily defined homologous point on the shells.

Eigenshape analysis (Lohmann and Schweitzer, 1990; MacLeod, 1999) of the resulting closed outlines was carried out using the Standard Eigenshape Morpho-tool notebook (ver. 2.6; Krieger, 2006) in Mathematica (ver. 7.0; Wolfram, 2008). All outlines were resampled to 300 coordinates during this process.

The number of axes generated by an eigenshape analysis is always one less than the number of specimens in that analysis. Therefore, the potential number of axes available to generate characters in a phylogenetic analysis using multiple specimens of many species is very large and the total number included will vary depending on the method used to select the cutoff point for inclusion. Here, it was assumed that where an axis explained less than 1% of the variation in the dataset, that axis' variation was noise. Fourteen axes were therefore included, thereby producing 14 continuous

characters in addition to the 275 informative DNA characters, giving a total of 289 phylogenetically informative characters in the total evidence matrix.

The eigenshape analysis defines new axes through the dataset, each of which corresponds to some portion of the variation in the original data and it is the position of a species along these new axes that is used here as the input into TNT (Goloboff et al., 2006; Goloboff et al., 2008) as this position describes the species' shape. However, these new axes are centered by definition on zero which produces negative eigenscore values for some specimens whereas TNT requires that all continuous character states be positive. To make the values suitable for analysis by TNT an arbitrary value of five was added to every eigenscore in the dataset to shift all values along the axis to make them positive. While this alters the absolute value of the eigenscores it preserves the relationships of each species as their relative position in shape space with respect to others is preserved and it is this relative position that is utilized in the phylogenetic analysis as TNT optimizes continuous characters as additive (i.e., ordered multistate) characters. TNT therefore optimizes the continuous characters in the same way as other additive characters by using Farris' (1970) algorithm for the downward-pass optimization which uses the intervals between the numerical values of the characters rather than the actual values themselves, allowing it to be applied directly to continuous numerical data (Goloboff et al., 2006). TNT allows ranges to be used as character states and in these cases during optimization, a step count of zero is used where the ranges overlap between taxa (i.e., where the means are statistically indistinguishable). Following the suggestion of Goloboff et a., (2006), one standard error around the mean was calculated for each species' scores (i.e., calculated using the scores of all the individual specimens of each species) on

each eigenaxis and this range was then used for the character states of continuous characters in the TNT matrix (see appendix 3) for a total evidence analysis.

Phylogenetic analysis: Molecular phylogeny and simultaneous analysis of total evidence matrix

The molecular matrix was compiled as a .tnt file after alignment described above. The total evidence matrix for analysis in TNT was compiled by adding the continuous characters generated to the DNA characters as a separate block within a .tnt file. All analyses were carried out in TNT (ver. 1.1; Goloboff et al., 2003). Both the molecular phylogeny and the total evidence tree were calculated using traditional parsimony analysis using 1000 tree bisection-reconnection (TBR; Swofford and Olsen, 1990) replicates where the ten shortest trees were held after each replicate and the random seed option was set to 0 (time); otherwise TNT's default settings were used. Memory was set to hold 10,000 trees and unsupported nodes were set to be collapsed (i.e., "rule 3" was implemented) so as to not show unsupported dichotomies. Uninformative characters were deactivated prior to each analysis. Bayesian and likelihood methods were not employed as the methodology described herein is designed to utilize TNT's implementation of continuous character analysis using parsimony.

Phylogenetic analysis: "Cladistic pseudofossil analysis"

In paleontology, the term pseudofossil is used to mean an object that may be mistaken for a fossil. However, a number of studies in the systematic literature (e.g., Jordan and Hill, 1999; Jordan and Macphail, 2003; Asher and Hofreiter, 2006) have begun to use the term to mean a species for which character data are removed prior to phylogenetic analysis to simulate including a species with limited character preservation, such as a

fossil species, in the analysis. Here the term "cladistic pseudofossil analysis" is used to indicate an analysis that uses modern taxa with molecular data to test the ability of the dataset to correctly reconstruct the phylogenetic relationships of a taxon lacking molecular data. To do so, after the total evidence tree is generated, a new matrix is constructed in which the molecular data for one taxon (the cladistic pseudofossil) is removed to simulate the inclusion of a fossil taxon for which only morphological characters are available. The cladistic pseudofossil analysis was then carried out using the same search parameters as used to generate the total evidence tree and the placement of the cladistic pseudofossil taxon in the new phylogeny is compared to its placement in the total evidence phylogeny.

Here, the ability of the morphological data to correctly place each of the ingroup taxa was evaluated by carrying out a cladistic pseudofossil analysis for each ingroup species (60 analyses in total). For each ingroup species, a new matrix was created by removing the molecular partition for that species. If the majority of pseudofossils can be placed successfully into the phylogeny using only the characters that would be available to be observed and measured from a fossil specimen, we can be confident that the methodology will allow actual fossils to be incorporated into a phylogenetic analysis with extant species.

Each bifurcation in the total evidence tree was given an identifying number to facilitate tracking of species that moved during the cladistic pseudofossil analysis (see Figure 1.3). A cladistic pseudofossil analysis was deemed a success if the pseudofossil remained within the same clade as it was placed in by the total evidence analysis. In some cases within the most derived clades, the criterion for success was relaxed somewhat to include semi-successful placement that included placing within the same major group, but not in the same sub-grouping as it was originally found

(e.g., *catus* moving to group with *tulipa* and *geographus* rather than with *magus*). Except for where the pseudofossil tree and total evidence were identical in topology, no single statistic was used to identify success in a pseudofossil analysis. Visual inspection of where a species had moved was the quickest method of identifying success, but examination of pseudofossil placement and potential disruption to the structure of the phylogeny was facilitated by using two of TNT's options: "Agreement subtrees" and "Compare groups" (see Goloboff et al., 2006; 2008).

"Agreement subtrees" produces a phylogeny comprised of only those taxa whose relationships have not altered between the total evidence and cladistic pseudofossil tree, allowing the taxa which have moved in the cladistic pseudofossil tree to be easily identified (i.e., it allows easy identification of those taxa that are incongruent between the total evidence tree and the pseudofossil tree). "Compare groups" indicates visually where the structure of the total evidence tree has been altered to become the cladistic pseudofossil tree by producing a phylogeny in which all taxa that are in agreement between trees are moved to a polytomy; and the new incongruous relationships are represented as branches showing where an alteration has occurred (e.g., see figure 1.4). The number of branches (b) that occur in a compare group tree (table 1.1) can be used as an indicator of how much disruption has occurred, with higher numbers of branches generally indicating more disruption.

Where the cladistic pseudofossil tree is identical to the total evidence tree, the "comparison phylogeny" is a complete polytomy and b=0. Where there are differences between the cladistic pseudofossil tree and the total evidence tree, these appear as nodes on the comparison phylogeny (positions indicated by an "x" on figure 1.4). A higher number of nodes (i.e., a high value of x) on the comparison phylogeny

Figure 1.3: Total Evidence Phylogeny. Roman numerals indicate clades that are well supported in Duda and Kohn's 2005 calmodulin phylogeny (assigned from top to bottom on that phylogeny). Numbers indicate clades assigned here to assist in tracking moving cladistic pseudofossils during cladistic pseudofossil analyses. CI=0.286, RI=0.436.

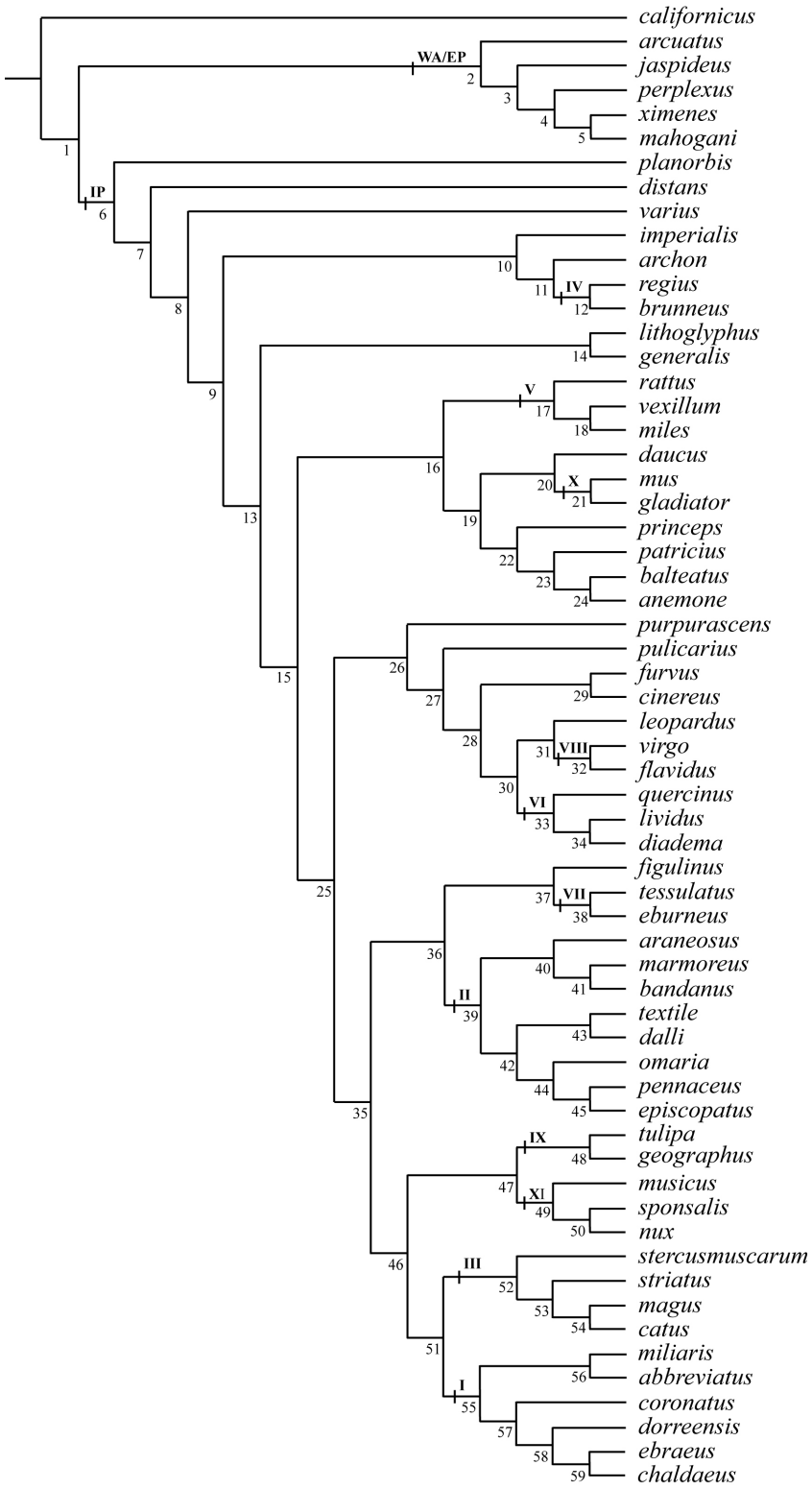
californicus
arcuatus
jaspideus
perplexus
ximenes
mahogani
planorbis
distans
varius
imperialis
archon
regius
brunneus
lithoglyphus
generalis
rattus
vexillum
miles
daucus
mus
gladiator
princeps
patricius
balteatus
anemone
purpurascens
pulicarius
furvus
cinereus
leopardus
virgo
flavidus
quercinus
lividus
diadema
figulinus
tessulatus
eburneus
araneosus
marmoreus
bandanus
textile
dalli
omaria
pennaceus
episcopatus
tulipa
geographus
musicus
sponsalis
nux
stercusmuscarum
striatus
magus
catus
miliaris
abbreviatus
coronatus
dorreensis
ebraeus
chaldaeus
WA/EP
IP
IV
V
X
VIII
VI
VII
II
IX
XI
III
I
1
2
3
4
5
6
7
8
9
10
11
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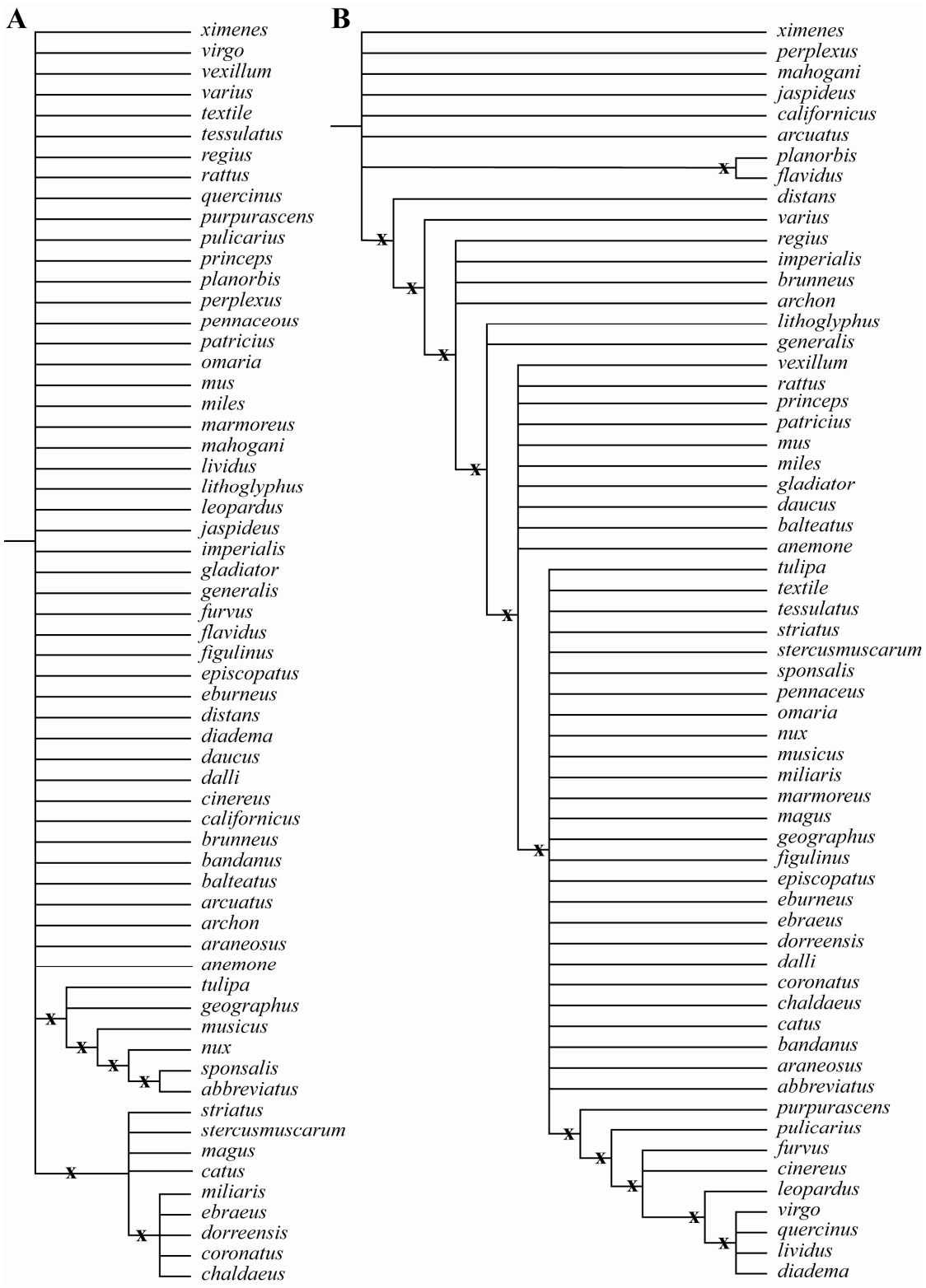
Figure 1.4: Comparison tree for cladistic pseudofossil analyses of A: *abbreviatus* and B: *flavidus*. In both cases, the number of branches produced is 2 (i.e., b=2). However, A has been classified as a successful cladistic pseudofossil analysis as the cladistic pseudofossil moved to a different clade within its major clade (number of disrupted nodes, x=6) whereas in B the cladistic pseudofossil moved further, causing more disruption (x=12).


A
ximenes
virgo
vexillum
varius
textile
tessulatus
regius
rattus
quercinus
purpurascens
pulicarius
princeps
planorbis
perplexus
pennaceous
patricius
omaria
mus
miles
marmoreus
mahogani
lividus
lithoglyphus
leopardus
jaspideus
imperialis
gladiator
generalis
furvus
flavidus
figulinus
episcopatus
eburneus
distans
diadema
daucus
dalli
cinereus
californicus
brunneus
bandanus
balteatus
arcuatus
archon
araneosus
anemone
tulipa
geographus
musicus
nux
sponsalis
abbreviatus
striatus
stercusmuscarum
magus
catus
miliaris
ebraeus
dorreensis
coronatus
chaldaeus
B
ximenes
perplexus
mahogani
jaspideus
californicus
arcuatus
planorbis
flavidus
distans
varius
regius
imperialis
brunneus
archon
lithoglyphus
generalis
vexillum
rattus
princeps
patricius
mus
miles
gladiator
daucus
balteatus
anemone
tulipa
textile
tessulatus
striatus
stercusmuscarum
sponsalis
pennaceus
omaria
nux
musicus
miliaris
marmoreus
magus
geographus
figulinus
episcopatus
eburneus
ebraeus
dorreensis
dalli
coronatus
chaldaeus
catus
bandanus
araneosus
abbreviatus
purpurascens
pulicarius
furvus
cinereus
leopardus
virgo
quercinus
lividus
diadema

indicates that the cladistic pseudofossil has moved further than where there are fewer nodes. Where a cladistic pseudofossil has moved out of its own clade and into another, a branch extending down to the basal polytomy is produced on the comparison phylogeny (see figure 1.4). It is possible for a cladistic pseudofossil to move a long distance and produce a few branches (e.g., if it moved from the top of the major group and down into a more basal clade as in figure 1.4b, as well as moving a short distance between clades within the major group as in figure 1.4a). If there are any nodes on the comparison phylogeny, b must by definition be at least one. Therefore, a combination of the number of incongruent branches found on the comparison phylogenies (b) and the number of nodes (x) was used as supporting information in an attempt to identify successful and less successful cladistic pseudofossil analysis results. In some cases the cladistic pseudofossil analysis caused disruption in parts of the phylogeny that the cladistic pseudofossil species had not moved to or from. These were counted as being successful where the topology of the clade in which the cladistic pseudofossil placed was not affected.

Successful cladistic pseudofossil analyses were found to occur where $b \leq 1$ (with some exceptions such as if the species has moved from a basal position to a crown group but other groupings remain congruent as with *C. planorbis* or *C, imperialis*). In rare cases where a species has moved only a short distance within a crown group, $b=2$ was also classified as successful as it places the cladistic pseudofossil within the correct parent group. In these cases, however, while the analysis is deemed successful the cladistic pseudofossil is further from its position in the total evidence phylogeny than in other successful analyses and may be considered semi-successful rather than truly successful. Cases where $b=2$ was considered to be successful were those in which the number of total x's on the comparison tree was low, but this is a less useful guide than

looking at the structure of the cladistic pseudofossil tree as often a high number of x's may be caused by movement within a small distance in a densely sampled crown group rather than large movements across the phylogeny. Where b≥3 the analysis was automatically classified as a failure as it indicates not only disruption to the cladistic pseudofossil's clade of origin and its new clade, but also disruption elsewhere in the tree. The absolute value of x is less useful as an indicator of success as, while a high b automatically results in a high x (e.g., *C. distans*), it is possible to have a low b and high x such as where a cladistic pseudofossil moved from a basal position up the phylogeny, such as with *C. planorbis*.

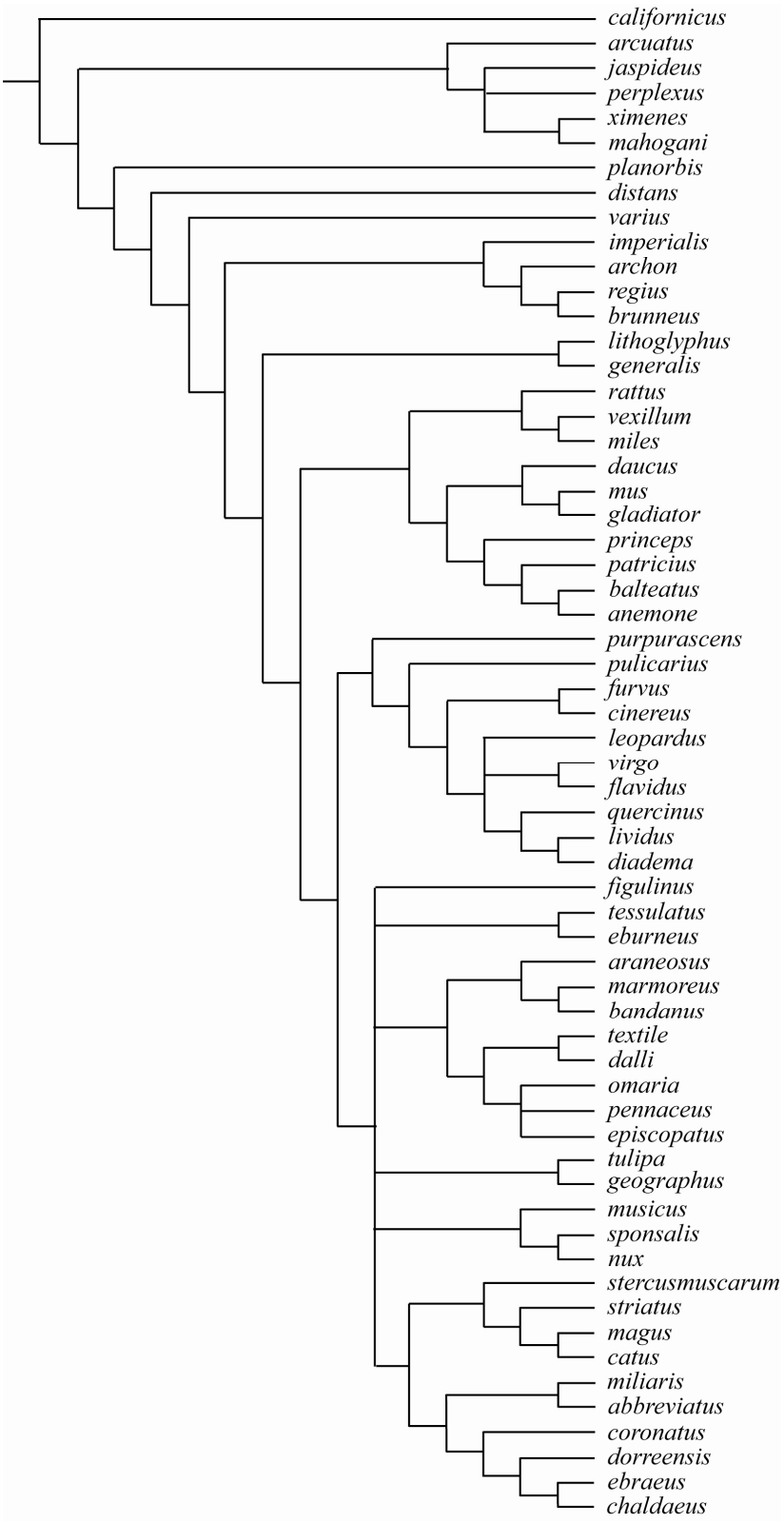
Results

The molecular phylogenetic analysis produced 24 equally parsimonious trees of length 1461 with, a CI of 0.343 and an RI of 0.566. A strict consensus tree can be seen in figure 1.5.

Figure 1.6 shows shape variation along these first three eigenaxes (see also figure 1.2). Axis one shows, from low to high scores along the axis, variation in the height of the spire across the axis from steep sided (*C. arcuatus*-like) to flattened (*C. leopardus*-like). Axis two shows variation in elongation of the body whorl of the shell from short and wide (*C. miliaris*-like) to thinner and more elongated and cylindrical (*C. geographus*-like) while axis three shows variation in the concavity/convexity of the spire from concave (*C. generalis*-like) to more rounded (*C. chaldaeus*-like).

The total evidence phylogeny is shown in figure 1.3. It has a length of 1469.841, a CI

Figure 1.5: Strict consensus of 24 phylogenies for calmodulin and 16s rRNA . CI=0.343 and RI=0.566


californicus
arcuatus
jaspideus
perplexus
ximenes
mahogani
planorbis
distans
varius
imperialis
archon
regius
brunneus
lithoglyphus
generalis
rattus
vexillum
miles
daucus
mus
gladiator
princeps
patricius
balteatus
anemone
purpurascens
pulicarius
furvus
cinereus
leopardus
virgo
flavidus
quercinus
lividus
diadema
figulinus
tessulatus
eburneus
araneosus
marmoreus
bandanus
textile
dalli
omaria
pennaceus
episcopatus
tulipa
geographus
musicus
sponsalis
nux
stercusmuscarum
striatus
magus
catus
miliaris
abbreviatus
coronatus
dorreensis
ebraeus
chaldaeus

of 0.286 and RI of 0.436. It produces the same major groups as the molecular phylogeny but the inclusion of the continuous characters has led to improved resolution. Using this combined matrix of calmodulin, 16s rRNA and continuous morphometric characters, the same major groupings reported by Duda and Kohn, 2005 were recovered, i.e., the major split between the Indo-Pacific and Western Atlantic/Eastern Pacific taxa and additionally all groupings with greater than 50% bootstrap support in the Duda and Kohn calmodulin tree (see roman numerals in figure 1.3). The molecular consensus tree produced from the calmodulin and 16s rRNA data is congruent with the total evidence tree, though not identical to it due to some differences in species relationships within the more derived groups that are resolved by the addition of the continuous morphological character data.

Table 1.1 shows a summary of the cladistic pseudofossil analyses, recording the CI and RI of each cladistic pseudofossil tree as well as their success or otherwise and b values. In addition, the clade location of the cladistic pseudofossil in each analysis is given, indicating where that cladistic pseudofossil moved to with reference to the total evidence tree. Initial inspection of the results suggests that only 38% (n=23) of the cladistic pseudofossil analyses successfully place a species into the phylogeny.

Discussion

While initial success rates may appear low, in most cases, the inability to place the cladistic pseudofossil correctly does not appear to be the fault of the continuous characters. There appear to be two main reasons for failure in the cladistic pseudofossil analyses: the molecular dataset and poor taxon sampling.

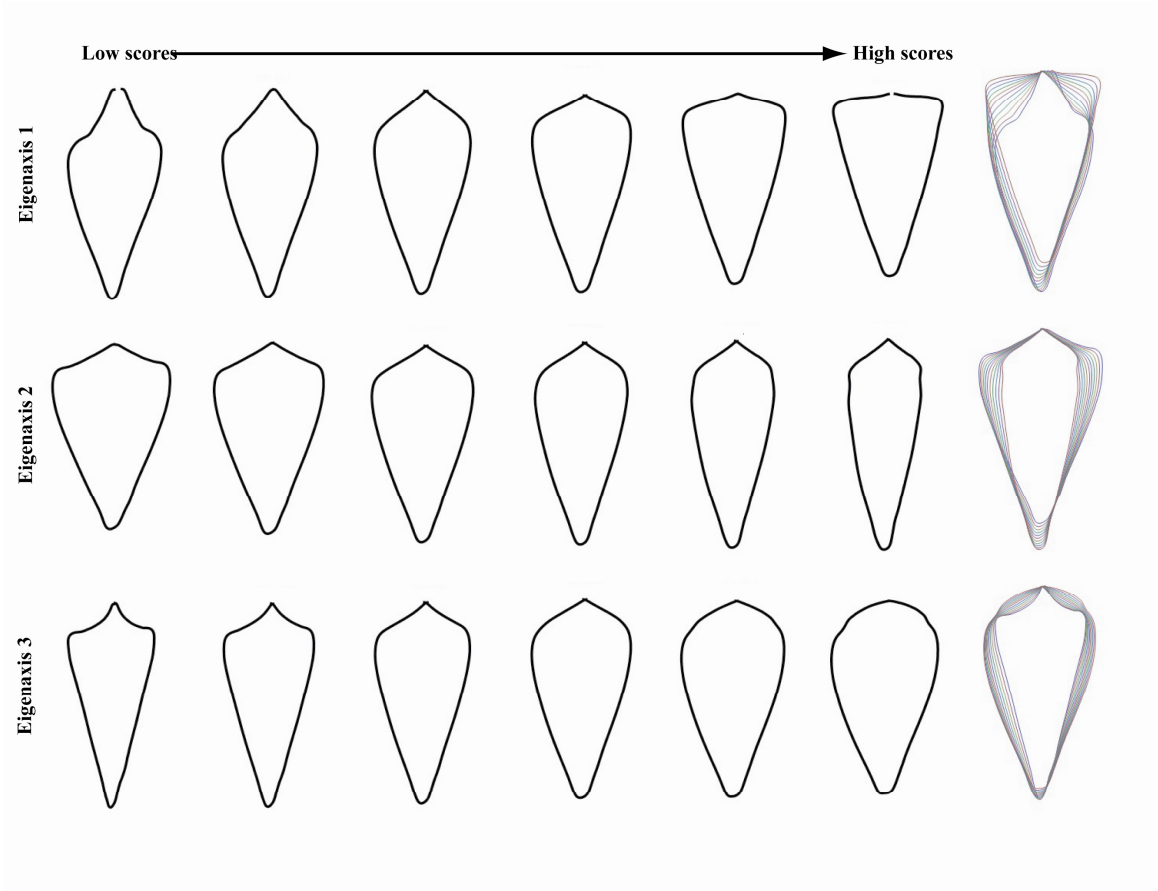


Figure 1.6: Shape models along eigenaxis one to three. Right most figure is a composite of ten models along the axis (including those shown in the figure) superimposed upon each other.

Quality of the molecular dataset

Seventeen of the species sampled here do not have well supported relationships based on the molecular data (three of these did form clades with other species in the Duda and Kohn (2005) phylogeny but with species that are not represented in this analysis), see Table 1.1. It would therefore be surprising, perhaps, if these taxa did place correctly during the cladistic pseudofossil analysis. Of the 43 species whose relationships are not suspect based on the molecular data, 53% are successfully placed in the cladistic pseudofossil analyses.

Factors besides the lack of support in the original calmodulin tree of Duda and Kohn, (2005), suggest that these taxa may be unstable for reasons unrelated to the morphological data set. However, these taxa were not removed from the total evidence analysis as this would further reduce taxon sampling. In 25% of cases when a cladistic pseudofossil moved out of the clade it was originally placed in, it grouped with a clade that contained one or more of the species that had no node support in the original calmodulin tree. In 19% (n=12) of the cladistic pseudofossil analyses (see table 1), disruption occurred outside of the clade that the cladistic pseudofossils moved to or from. Of these, seven were species whose placements are poorly supported by the original molecular data, suggesting that the placement of these taxa in the total evidence tree was suspicious. This agrees with Wien's 2003b finding that taxa with missing data often do not negatively impact relationships across the phylogeny.

Taxon sampling

Given the size of the *Conus* genus (over 500 extant species; Röckel et al., 1995) it is clear that there are many species not included in this study. More so, despite the efforts made to sample as many taxa as possible from Duda and Kohn's (2005) 138 species list, this analysis still contains only half of the total species used in their study, which itself was a small portion of the total number of *Conus* species. Some of the unsuccessful cladistic pseudofossil analyses may therefore be attributed to poor taxon sampling in parts of the phylogeny.

In this study, many of the unstable cladistic pseudofossil taxa place into clades that are less densely sampled in this study, e.g., clade 11 and 14 (figure 1.3). Some of this instability is due to the poor taxon sampling of these clades within the genus. While increased taxon sampling is known to increase the accuracy of phylogenetic trees (e.g., Pollock et al., 2002; Zwickl and Hillis, 2002; DeBry, 2005), there is little that can be done to remedy this problem in this study until more well-preserved specimens are available for some of those species that were not included due to poor representation in museum collections. Here, efforts were made to maximize the number of taxa included from the reference molecular phylogeny (Duda and Kohn, 2005), but problems caused by poorly sampled regions of the tree in the original molecular dataset are impossible to eliminate until relevant molecular data are available for more species in these clades.

Homoplasy

Rarely was the movement of a cladistic pseudofossil due to shell homoplasy. An example where this does seem to have been the case, however, was for *C. dorreensis*, where the cladistic pseudofossil moved from the Indo-Pacific clade with *C. ebraeus* and *C. chaldaeus* into the western Atlantic/eastern Pacific clade with *C. ximenes*. This is due, presumably, to the extreme similarity in body whorl shape between these two species. This similarity is likely due to homoplasy, as sequence data consistently place *C. dorreensis* in the Indo-Pacific clade. Had other data been integrated into the total evidence tree, such as color patterns (e.g., see the matrix of Hendricks, 2005) or other traditional shell character data (e.g., number of protoconch whorls), the cladistic pseudofossil placement of *C. dorreensis* may have been less radically different. This is also true in other cases where the relocation of the cladistic pseudofossil was less radical and less obviously linked to homoplasy than in the case of *C. dorreensis*. This entire analysis has been carried out using only a molecular partition and fourteen characters generated from geometric morphometric analysis of total shell shape which accounted for only 5% of the characters in the matrix. The inclusion of other traditional characters, shell color pattern information and perhaps other potential sources of information that might also be treated using geometric morphometrics, such as the shape of the subsutural flexure that is known to have a taxonomic signal (Smith, 1930; Hendricks, 2009), may provide more stability within the matrix.

Conclusions

The method described here allows more than half of the species treated as cladistic pseudofossils to be successfully placed into the clade to which the total evidence tree

suggests they belong. Where failures occur, it does not, except in rare cases, appear to be due to the continuous characters, but rather instability in the relationships suggested by the molecular data. This instability is partly due to inadequate taxon sampling and partly due to the molecular data themselves. In addition, the definition of success used here is quite conservative and a looser definition of success would also allow valuable information to be gained from the results of a phylogenetic analysis. The ability to place a true fossil with slightly less accuracy than achievable here should also be viewed as a success if it provides more information about which extant species it is related to than was previously known, even if the exact sister group relationships remain unclear.

This level of success has been possible using only 14 continuous characters (5% of the total evidence matrix). There are a number of other characters in *Conus* that carry, or potentially carry, phylogenetic signal (e.g., radular and other anatomical characters, color patterns, other parts of the shell morphology such as the subsutural flexure shape etc.) which have not been included. If such other characters were integrated into the analysis, the resolution, and therefore the power, of the method to place cladistic pseudofossil and fossil taxa correctly would in all likelihood be further enhanced.

There has in the past been a perception (e.g., Patterson, 1981; Hulsenbeck, 1991) that the incorporation of extinct taxa lacking preserved molecular or non-mineralized characters in phylogenetic analyses of extant taxa is thwarted by the quantity of missing data present in the matrix for the extinct taxon which prevents that taxon from placing correctly. However, studies have shown (Novacek, 1992; Kearney, 2002; Wiens, 2003a; Wiens, 2006; Hermsen and Hendricks, 2008) that cladistic matrices with one or more extinct taxa with large amounts of missing character data do not

automatically mean that those taxa will not occupy well resolved positions in phylogenetic hypotheses. It is instead more relevant that the characters that can be coded are characters important to the phylogenetic structure (see also Corbett et al., 2007 for further discussion of the inclusion of fossils into phylogenetic analyses of extant taxa). This, combined with the success of this study, indicates that future studies will be able to successfully incorporate multiple taxa that lack molecular data into a total evidence matrix.

This case study has successfully used *Conus* as a test case for incorporating taxa with limited discrete character data into total evidence analyses. This success suggests that further work will allow questions about evolution in the genus to be addressed. Beyond *Conus*, however, this methodology also has great potential for application to other gastropod groups that have previously lacked enough discrete characters for phylogeny reconstruction and for which, therefore robust phylogenies have never been constructed. Additionally, many other invertebrate taxa also suffer from a lack of discrete morphological characters. With some adaptation to the relevant homologous structures in other groups, this methodology should be widely applicable across phyla for generating phylogenetic hypotheses where morphological characters have previously been limited and molecular data is unavailable.

While constructing phylogenies for these taxa is useful in itself, phylogenies are also essential for many other studies. Many groups that lack discrete character data, such as the gastropods, have excellent fossil records due to their mineralized hard-parts. They therefore present otherwise ideal groups in which to address a range of macroevolutionary questions. Once robust phylogenetic hypotheses are established for groups previously lacking them it will begin to be possible to address a wide range

of macroevolutionary questions by integrating fossil taxa into phylogenetic analyses to investigate their evolutionary histories.

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CHAPTER 2

PHYLOGENETIC ANALYSIS OF THE NEW ZEALAND GASTROPOD GENERA *ZEACOLPUS* AND *STIRACOLPUS* (TURRITELLIDAE) USING CONTINUOUS CHARACTERS

Abstract

Phylogenetic analysis of two genera or New Zealand turritellid gastropods was carried out using ten discrete characters in combination with a suite of continuous characters generated from eigenshape analysis of shell shape. Phylogenies were generated using a variety of weighting schemes. The results support the individual generic status of *Zeacolpus* and *Stiracolpus* but suggest species relationships that are unlike those previously suggested by non-phylogenetic methods. Significant ghost ranging of many species is also implied.

Introduction

The turritellid gastropods are a highly diverse group (estimated 2000 species; Allmon, 2004), have a wide geographic distribution throughout the Cenozoic fossil record and are often found in high abundances. The turritellids therefore have potential as a group for the study of macroevolutionary questions (e.g., Allmon, 1994; 2007), and the New Zealand representatives of the group in particular may be well suited for such studies. Turritellids are an important component of the New Zealand molluscan fauna (Marwick, 1957a; 1957b; 1971), with twelve genera represented in the New Zealand

fossil record (Marwick, 1957b), three of which (*Maoricolpus*, *Zeacolpus* and *Stiracolpus*) still have living representatives. New Zealand Cenozoic sediments contain a diverse and abundant fossil mollusk fauna (e.g., see Beu and Maxwell, 1990), the richest in the Southern Hemisphere and the faunas show a high degree of endemism, suggesting that many evolutionary events have occurred *in situ* with limited impact from immigration (Crampton et al., 2006a). These faunas have been well studied (e.g., Fleming, 1966; Beu, 1990, Beu, 1990; Beu and Maxwell, 1990) and have been used extensively in a number of different types of study including biostratigraphy, paleoenvironmental reconstruction, and diversity studies (e.g., Fleming, 1944; Beu, 1969; Beu, 1974; Vella et al., 1975; Crampton et al., 2003; Cooper, 2004; Hendy and Kamp, 2004; Kamp et al., 2004; Crampton et al., 2006b; Crampton et al., 2006a; Hendy, 2009; Hendy et al., 2009). The stratigraphic, depositional, and environmental context of these faunas is therefore well understood, particularly for the Pliocene onwards (e.g., Carter, 2005; Cooper, 2004; Naish, 2005)

To address many macroevolutionary questions, however, more than an excellent fossil record is required; a phylogeny is essential. However, producing robust phylogenetic hypotheses for turritellid gastropods has proved problematic in the past. Despite obvious diagnostic differences in shell morphology between species, the continuous variation of this shell morphology has not been easy to break down into discrete character states (e.g., see Allmon, 1996). This problem is not restricted to the turritellid gastropods, but is prevalent in many other gastropod groups (e.g., Wagner, 2001; Hendricks, 2005) as well as many other invertebrate taxa.

As a result of this lack of easily coded shell characters, previous efforts at resolving species-level relationships in turritellids have been limited to using more or less

stratophenetic methods (Gingerich, 1979) in which species relationships are guided by stratigraphy and, to a lesser extent, geography as much as by morphological similarity (e.g., in the Eocene and Paleocene Coastal Plain (Allmon, 1996) or with the species of *Stiracolpus* Finlay, 1927 in New Zealand (Marwick, 1957a)). The only molecular phylogenetic study of turritellids (Lieberman et al., 1993), sampled only nine species (of around 170 living species; Allmon, 2004) from two genera. It therefore does not form an adequate framework for macroevolutionary studies. There is scope for genetic work in the New Zealand turritellids as there are a number of species living around the coast today representing three genera (*Stiracolpus*, *Zeacolpus* and *Maoricolpus*). Currently, however, molecular data for these species are lacking, with only two modern species having been sampled (*Stiracolpus pagoda* Reeve, 1849 and *Maoricolpus roseus* Quoy and Gaimard, 1834, though both *M. roseus roseus* Quoy and Gaimard, 1834 and *M. roseus manukauensis* Powell, 1931 subspecies have been used), with approximately six thousand base pairs of the mitochondrial genome having been sequenced (S. Hills, Massey University at Palmerston North, pers. comm. 2008).

Recent advances in utilizing continuous character data in phylogenetic analyses have opened up new possibilities for including shell morphology in phylogenetic matrices. The implementation of Farris' (1970) algorithm in the software Tree analysis using New Technology (TNT; Goloboff et al., 2003a) has allowed continuous characters to be included directly into a phylogenetic analysis without breaking them into discrete character states. This has allowed some studies to begin to include length measurements into phylogenetic analyses (e.g., Hendrixson and Bond, 2009;Vega et al., 2009) As an extension of this, the use of the geometric morphometric methodology of eigenshape analysis (Lohmann and Schweitzer, 1990; MacLeod,

1999), allows shell shape to be described in great detail and included into an analysis in TNT as continuous shape characters.

Methodologies designed to specifically incorporate shell shape must be applied with caution in turritellids due to homoplasy in shell shape. The problem of homoplasy in is particularly problematic at taxonomic levels above the genus as it is clear that there is homoplasy in general shell morphology between genera (Allmon, 1994; 1996; Kotaka, 1978), with some common morphologies occurring in many groups. Within a genus the problem of homoplasy is less severe. Though similar gross morphologies may occur due to the common ancestry of the species in the genus, there is variation of finer scale morphology such as the spiral ornament that is less homoplasious.

The method of integrating shape variation in the phylogenetic analysis used here is similar to that of González-José et al., (2008) but utilizes eigenshape analysis rather than landmark analyses. The definition of homologous points on gastropod shells between species and through ontogeny is difficult but the use of semi-landmarks in an eigenshape analysis allows shape to be described without having to define strict homologous points between the shapes in question; the shape being described is homologous even if there are no homologous points within it.

This study aims to produce a phylogeny for two of the New Zealand genera of turritellids -- *Zeacolpus* Finlay, 1926 and *Stiracolpus* Finlay, 1927, two of the most diverse of the New Zealand turritellid genera -- using both traditional shell characters and continuous characters based on geometric morphometric descriptions of shell shape.

Methods

Generic Level Phylogenetic Analysis

To establish that *Zeacolpus* and *Stiracolpus* are not a monophyletic group but rather individual genera, a phylogeny for *Turritellidae* was generated using the genera of Marwick, 1957b and *Kapalmerella* Allmon, 2005. Characters were taken from Allmon, 1996 (see Allmon 1996, table 1), though the ontogenetic sequence of spiral cord development was coded as three discrete non-additive characters rather than as one character. Phylogenetic analysis was performed in TNT using parsimony. One thousand tree bisection-reconnection (TBR; Swofford and Olsen, 1990) replicates were carried out with the ten shortest trees saved after each replicate. Memory was set to hold 10,000 trees and unsupported nodes were set to be collapsed so as to not show unsupported dichotomies, and uninformative characters were deactivated. The random seed was set to 0. Otherwise, TNT's default settings were used.

Stiracolpus *and* Zeacolpus *Phylogenetic Analyses*

The genus-level taxonomy of New Zealand turritellids has varied considerably over the years with *Zeacolpus* having been used as a catch-all genus. Various species from other genera have been assigned to *Zeacolpus* at different points (e.g., several species of *Tropicolpus* Marwick, 1931 and *Amplicolpus* Marwick, 1971), and some genera have been variously assigned as sub-genera (e.g., *Leptocolpus* Finlay and Marwick, 1937 and *Stiracolpus*) or separate genera in their own right. The species-level taxonomy of the New Zealand turritellids, however, is relatively robust, having been largely defined by one worker (e.g., Marwick, 1957a; 1957b; 1971). It is nevertheless

possible that there are fewer species, each of which exhibits a wide range of morphological variation (Beu. pers. comm.) but this cannot currently be firmly distinguished using shell based criteria and will require the application of genetic techniques.

Specimens used in this analysis came from the collections of the Institute of Geological and Nuclear Sciences, New Zealand (GNS) and the Paleontological Research Institution (PRI).

Ingroup taxa

The *Stiracolpus* analysis included 23 species of *Stiracolpus* (77% of species in the genus), the *Zeacolpus* analysis included 18 species (78% of species in the genus), table 2.1 and figures 2.1 and 2.2. This includes all species for which adequately preserved material was available (i.e., specimens which could be identified to species level and for which undamaged whorl profiles were visible).

Outgroup taxon

Maoricolpus roseus (Quoy and Gaimard, 1834) was used as the outgroup. Other potential outgroups included the Recent *Turritella terebra* (Linnaeus, 1758) and *Leptocolpus semiconcavus* (Suter, 1911), a fossil from the New Zealand Eocene that has previously been placed in the genus *Zeacolpus* and other New Zealand fossil turritellid species. *L. semiconcavus* was not used because no protoconch (the larval shell that forms the very tip of the shell, see figure 2.3) is known and all the available specimens were fragmentary, making whorl number unclear. *M. roseus* was selected

Table 2.1: Species of *Stiracolpus* and *Zeacolpus* used here. Numbers indicate the number of available specimens of suitable quality for the generation of eigenshape-based continuous characters. The name *S. murdochi* here is used for an unpublished, morphologically distinct form that Marwick (1957a) believed to be a hybrid of *S. delli murdochi* and *S. shepherdi*.

***Stiracolpus* species**	**No. of specimens**	***Zeacolpus* species**	**No. of specimens**
Stiracolpus ahiparanus Powell 1927	9	*Zeacolpus. awamoaensis* Marwick, 1971	10
S. ascensus Marwick 1957	14	*Z. flemingi* Marwick, 1971	3
S. blacki Marwick 1957	1	*Z. fyfei* Marwick, 1931	3
S. delli Marwick 1957	7	*Z. gagei* Marwick, 1971	1
S. *delli granti* Marwick 1957	1	*Z. greggi* Marwick, 1971	4
S. *delli murdochi* Marwick 1957	6	*Z. keari* Marwick, 1971	3
S. delli velli Marwick 1957	2	*Z. lawsi* Marwick, 1971	2
S. huttoni ohopeus Marwick 1957	3	*Z. lornensis* Fleming 1966	8
S. kawaensis Laws, 1934	3	*Z. nisseni* Marwick, 1971	2
S. knoxi Marwick 1957	5	*Z. opoitius opoitius* Fleming 1966	2
S. mixtus Finlay, 1930	2	*Z. opoitius taranakiensis* Fleming 1966	2
S. murdochi	3	*Z. peteri* Marwick, 1971	2
S. nannulus Marwick 1957	4	*Z. pukeuriensis* Marwick, 1934	5
S. pagoda Reeve, 1849	2	*Z. taranakiensis* Marwick 1965	2
S. procellosus Marwick 1957	5	*Z. vittatus* Hutton 1873	5
S. propagoda Laws, 1940	1	*Z. wharekuriensis* Marwick, 1971	7
S. quenelli Marwick 1957	2	*Z. willetti* Marwick, 1971	3
S. robinae Marwick 1957	1	*Z. woodhousea* Marwick, 1971	3
S. shepherdi Marwick 1957	1		
S. symmetricus Hutton 1873	3		
S. uttleyi Marwick 1957	3		
S. vigilax Marwick 1957	2		
S. waikopiroensis Suter 1927	1		

Figure 2.1: *Stiracolpus* species. a) *ahiparanus* b) *ascensus* c) *blacki* d) *delli* e) *delli granti* f) *delli murdochi* g) *delli velli* h) *kawaensis* i) *knoxi* j) *mixtus* k) *murdochi* l) *nannulus* m) *quenelli* n) *robinae* o) *pagoda* p) *symmetricus* q) *uttleyi* r) *vigilax* s) *waikopiroensis*.

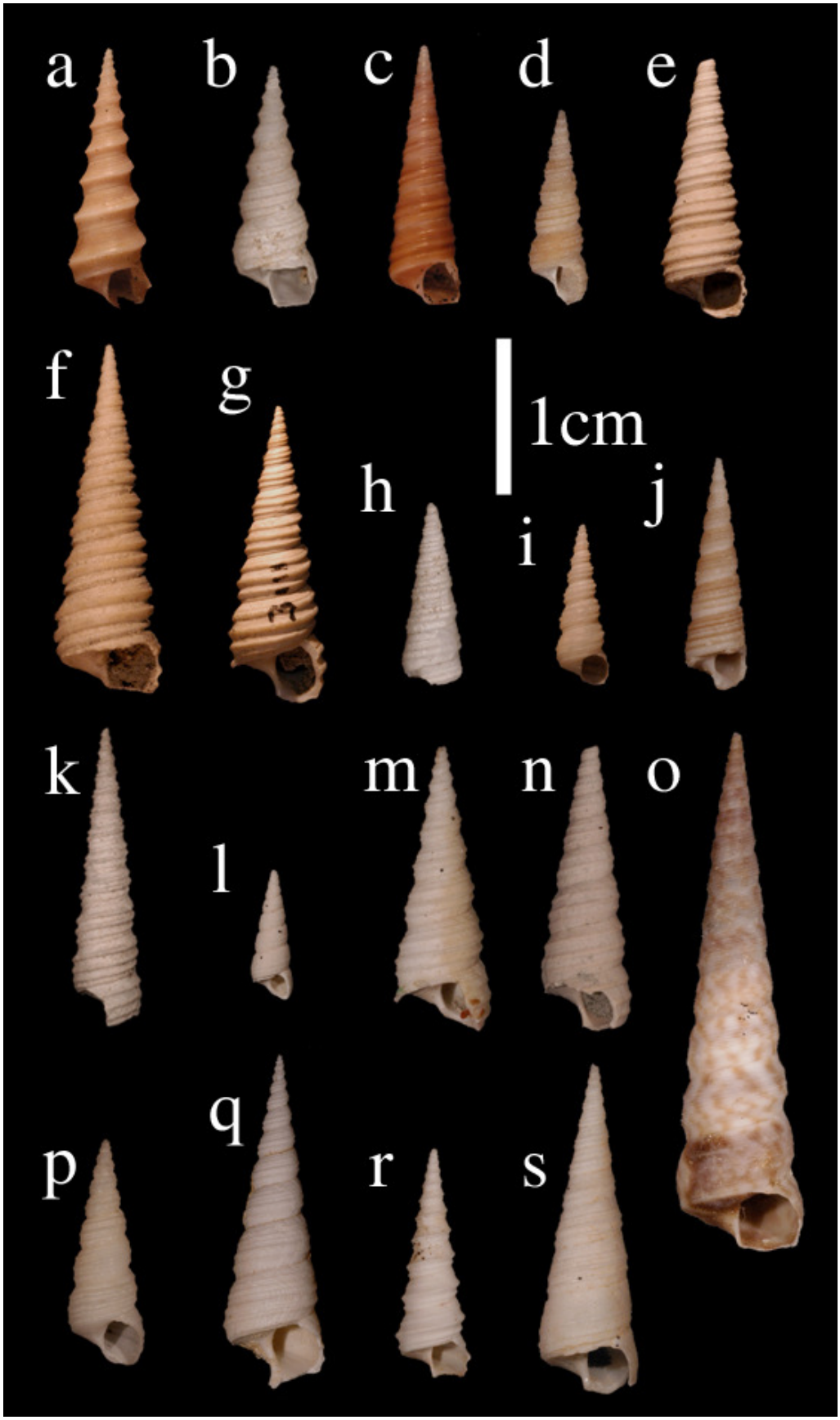
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Figure 2.2: *Zeacolpus* species. a) *awamoaensis* b) *flemingi* c) *fyfei* d) *greggi* e) *keari* f) *lawsi* g) *nisseni* h) *opoitius taranakiensis* i) *pukeuriensis* j) *taranakiensis* k) *vittatus* l) *willetti* m) *woodhousea*.


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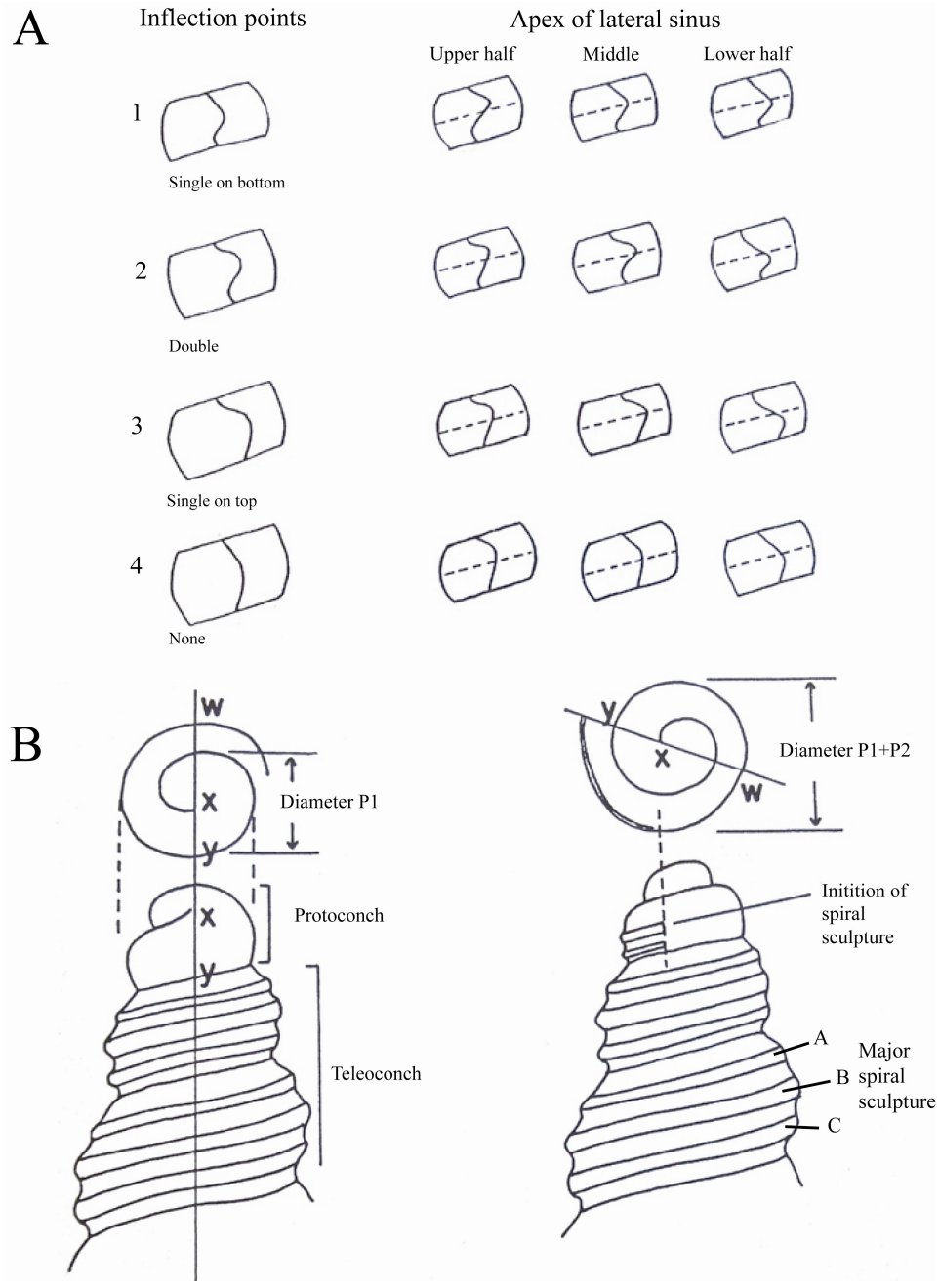
Figure 2.3: A) Lateral sinus shape classification. The lateral sinus reflects the shape of the rim of the shell's aperture (see the aperture rim of the shells pictured in figure 2.1, 2.2 and 2.4) at the point at which that portion of the shell was deposited. This is often referred to as a growth line as the shell is deposited incrementally at this edge. As the aperture of the shell is frequently broken post-mortem such that its shape is often indistinguishable, the shape of the sinus on the body whorl is used instead. B) Protoconch and spiral ornament appearance. The protoconch (larval shell)/teleoconch (adult shell) boundary is marked by the appearance of the spiral ornament of the shell. The number of protoconch whorls is counted spirally from the origination point (point X) to the initiation of spiral sculpture, where X-Y is half a whorl, X-W is one whorl. Order of origination of the spiral ornament, A, B and C, counted from first appearance of the spiral sculpture. Illustrations adapted from Allmon, 1996 figures 4 and 10.


A
Inflection points
Apex of lateral sinus
Upper half
Middle
Lower half
1
Single on bottom
2
Double
3
Single on top
4
None
B
W
X
Y
Diameter P1
Protoconch
Teleoconch
Diameter P1+P2
Initition of spiral sculpture
A
B
C
Major spiral sculpture

over *T. terebra* as it occurs in the New Zealand fossil record as well as around the coast of New Zealand today, and the protoconch is known. Additionally, *M. roseus* is more similar in size to *Zeacolpus* and *Stiracolpus* than *T. terebra*, which is both larger and has a very different apical angle and expansion rate and has a much greater number of whorls (up to an estimated 27 as compared to the estimated maximum of 20 in *Zeacolpus* and 15 in *Stiracolpus*). *M. roseus* was chosen over other New Zealand fossil turritellids as it is more similar to the morphology of the ingroups than, for instance, a species of *Tropicolpus* Marwick, 1931. It has been suggested that the genus *Haustator* Montfort, 1810, may have given rise to both *Zeacolpus* and *Stiracolpus* (Marwick, 1957b; Beu. pers. comm.) in two separate instances of immigration into New Zealand. This genus was not used here as an outgroup as too little material was available.

Generation of continuous characters from shell shape

Morphological change through ontogeny has in the past been described as an important diagnostic feature of species (e.g., Marwick, 1957a). To incorporate variation in shape through ontogeny, the shape of the whorl profile is used. The term "whorl" as used here refers to one 360º portion of shell growth (figure 2.4). The whorl profile is the shape of the edge of a whorl when viewed from the side of the shell. Whorl number was counted from the protoconch/teleoconch boundary i.e., where the larval shell ends and the adult shell beings, marked by the onset of spiral ornamentation (figure 2.3). Each successive whorl profile was taken at 360º intervals from the first to the last full teleoconch whorl, with each profile being labeled 1 to *n*. Not only does *n* vary between species, but individual specimens within species display different numbers of whorls due to age and breakage. Each whorl was assumed to be

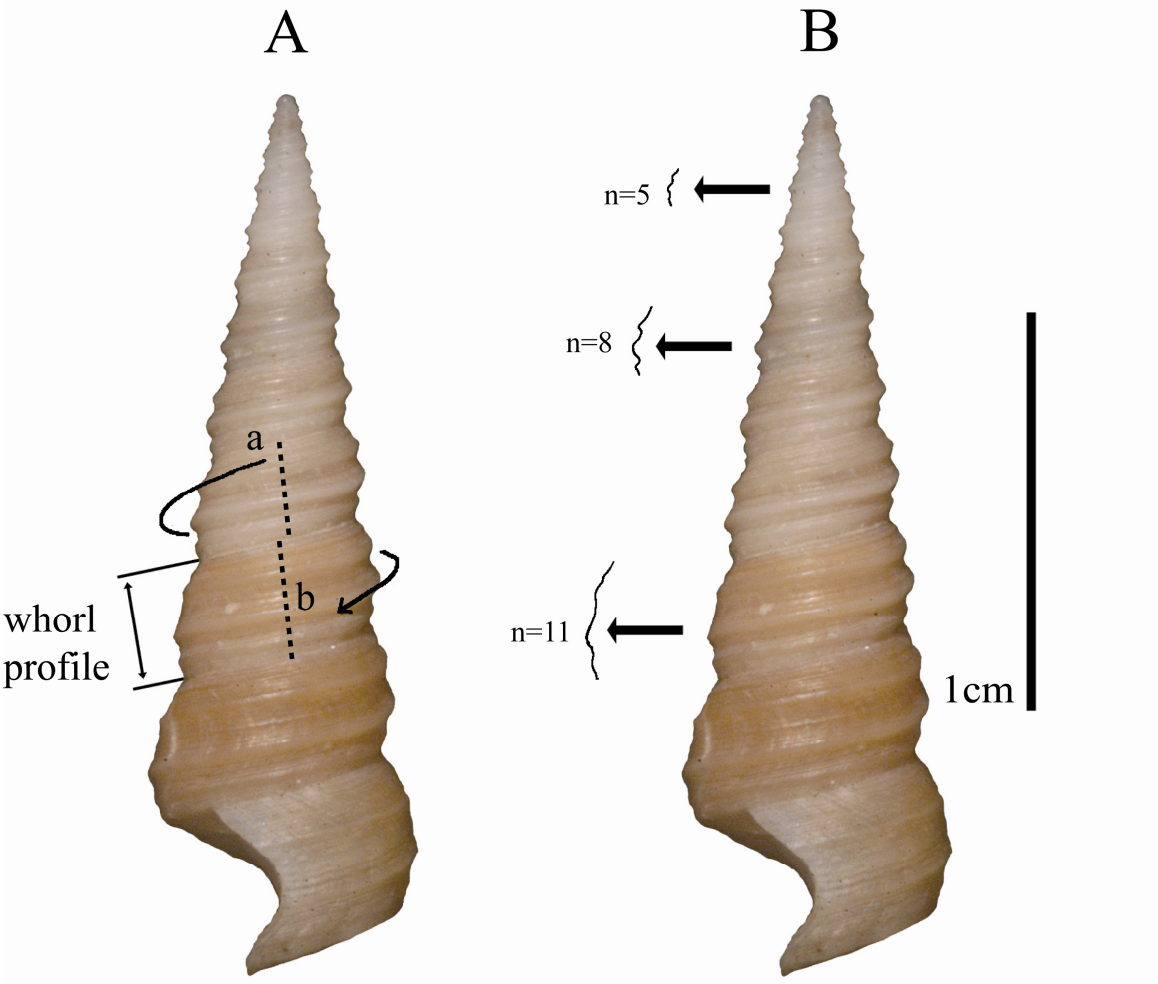


Figure 2.4: A) One whorl is 360º of rotational growth indicated here as starting at line a and ending at line b. Arrow indicates direction of growth. The whorl profile is the edge of the whorl as viewed from the side, the top and bottom of the profile are defined by the suture, i.e., where the whorl in question meets those above and below it indicated (positions indicated by solid black lines). B) The shape of the left profile of each whorl is traced, here three (the fifth, eighth and eleventh) have been shown for illustration purposes.

a homologous unit between species, such that whorl 7 of e.g., *Stiracolpus symmetricus* can be compared with whorl 7 of e.g., *S. ahiparanus* (figure 2.4). Some specimens did not include the protoconch/teleoconch boundary (i.e., the point at which ornamentation begins, see figure 2.3) due to breakage. In these cases, the whorl number of the first full whorl present was estimated by comparisons to the whorl size and profile shape of species for which the boundary is present (e.g., see Morris and Allmon, 1994). In this dataset, some fossil *Zeacolpus* species are represented only by fragments of the teleoconch and no protoconchs are known. In these cases, the first full whorl number of each specimen was estimated by comparison with other *Zeacolpus* species.

A gastropod shell its whorl profiles are complex structures made up of a range of continuous characters. In the past it has proved difficult to incorporate shell characters into phylogenetic analyses due to the difficulty of breaking these continuous characters down into discrete character states. The geometric morphometric method of eigenshape analysis (Lohmann and Schweitzer, 1990; MacLeod, 1999) can be used to describe the continuous shape variation of a gastropod shell and then incorporate that information into a phylogenetic analysis. To capture this shape data images of individual shells were captured such that the lens of the camera was parallel to the coiling axis of the shell. Each image was adjusted to the same scale such that the smallest teleoconch whorl's height was at least 50 pixels. This makes the traced outline of the profile at least 50 pixels long which will allow it to be made up of at least 50 coordinate points when the line is converted to coordinate points. As each progressive whorl is larger than the previous one there are therefore more coordinate points in each successive whorl. As an eigenshape analysis requires all curves to have the same number of coordinates all of the raw digitized curves were resampled to a

standard number of coordinates (the minimum number in the dataset) prior to the eigenshape analysis being performed. Ensuring each profile was scaled to be larger than a minimum height ensured that when the curves were resampled there were at least 50 points per curve. While it is possible to resample a curve to fewer points, it is not possible to increase the number as this adds points that are not part of the original shape, thereby altering it. While having more points in each curve to delineate the shape of each profile would be desirable, the image sizes required to do this proved prohibitive.

The left profile of each whorl of each specimen was traced in Photoshop (ver. 6.0; Adobe, 2000) using a digital tablet producing an open curve (see figure 2.4) that was exported as a jpeg file. Each whorl profile curve was converted to coordinate points, using code written in IDL (ver. 5.6; ITT Visual Information Solutions, 2002). Where the profile was damaged or obscured (e.g., by epibionts), that whorl was excluded from the series for that specimen. The first whorl traced was that immediately after the teleoconch/protoconch boundary.

Phylogenies were estimated for both *Zeacolpus* and *Stiracolpus* separately. Therefore, two separate eigenanalyses were carried out: 1) *Zeacolpus* species and the outgroup; 2) *Stiracolpus* species and the outgroup. Both eigenshape analyses were carried out using the Standard Eigenshape morpho-tool notebook (ver. 2.6; Krieger, 2006) in Mathematica (ver.7.0; Wolfram, 2008). The number of raw coordinate points in the whorl profile curves varied from 79 for the smallest of the immediately post-protoconch whorls (whorl 1) which are often only a few mm high to 5585 for the largest of the teleoconch whorls. The minimum number of coordinate points in the *Stiracolpus* dataset was 119, the minimum in the *Zeacolpus* dataset was 79. Every

curve was resampled during the eigenshape analysis to the minimum number in that dataset.

Eigenshape analysis is analogous to principal components analysis (using length data) or relative warps analysis (using landmark data). The eigenshape analysis defines a set of new axes through the dataset, each of which corresponds to some independent portion of the variation in the original data. These axes describe a shape space that encompasses the total shape variation in the input dataset Any shape included in the dataset occupies a point in the shape space that can be described by a set of multidimensional coordinates on these axes; these coordinates are the eigenscores generated by the eigenanalysis for each whorl profile included in the analysis. If the coordinates on each axis are known for that specimen, its shape can be reconstructed by summing the shape component expressed by the position of that species on each axis. The relative position of two individual shapes along each axis therefore indicates the relative difference in the shape of each. When including multiple individuals of a species that species therefore occupies an area of the shape space defined by all of its individuals (figure 2.5). Similarly, the relative shape of two species or whorls with respect to each other is described by the relative positions of each "cloud" of individuals.

It is the position of each whorl of each species along each axis described by these numerical coordinates that is used here as the input into the phylogenetic analysis in TNT (Goloboff et al., 2003a; Goloboff et al., 2006; Goloboff et al., 2008b) rather than length measurements that describe more basic shape parameters. Each whorl profile, a shape composed of variation in strength and position of shell ornamentation, is treated here as a complex of characters. The matrix of continuous characters produced in this

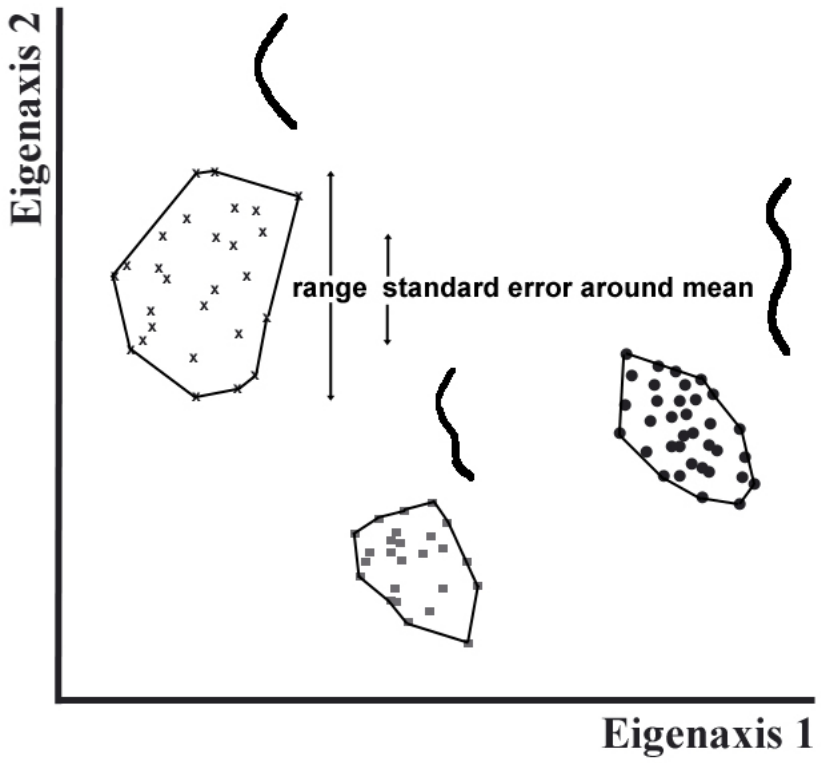


Figure 2.5: Example of an eigenplot showing three hypothetical whorl profiles varying along axis one. Each point on the plot represents one whorl profile. The shape of the whorl varies from a simple curve at low values to a biconcave curve at high values. The three species occupy separate areas of shape space defined by the most disparate morphologies of each species and each have a fixed position with respect to the others. The standard error around the mean of the range along each axis (shown here for one species on axis 2) is used as the range of the GM-continuous character for the phylogenetic analysis.

manner is made up of blocks of characters; each block describes the shape variation of one whorl number and is made up of eigenscore data from as many eigenaxis as necessary to describe the shape variation in the dataset.

The number of axes generated by an eigenanalysis is dependent on the number of specimens in the analysis. Though the combination of all the axes describes the total shape variation in the dataset, as the number of specimens increases at some point the variation explained by later axes becomes very small and can be considered noise. Here, all axes explaining greater than 1% of the shape variation in the dataset were used to construct the continuous character matrix. In this dataset this 1% cut off was at eigenaxis 21 for both individual genera and 25 for the combined analysis. A maximum number of 16 whorls occurred in the *Stiracolpus* dataset and 20 in the *Zeacolpus* and combined datasets, producing a total of 336 characters based on the eigenshape analysis for the *Stiracolpus* matrix, 420 for the *Zeacolpus* matrix and 500 for the combined analysis. These continuous characters are called GM-continuous characters for the rest of this paper to distinguish them from continuous characters being used to quantify measurements that have traditionally been broken down into discrete characters such as shell height.

In all cases where there were enough specimens, the range of the GM-continuous character used was one standard error around the mean value of the scores for whorl *n* of each species. Where only two profiles were available, both of those scores were used as the minimum and maximum for the range, and where only one profile was available its score was used as a single value without a range. To make all scores positive as required by TNT, 5 was arbitrarily added to each eigenscore before the calculation of standard errors was made. This alters the absolute values of the

eigenscores but not the relative position of each species and it is the position and degree of overlap between the continuous characters generated from the eigenscores that is relevant to the phylogenetic analysis of those characters not their numerical values (Farris, 1970; Goloboff et al., 2006).

Many species were missing whorls, either because all earlier or later whorls were missing due to breakage or because that species only grew to a smaller number than others (fully adult individuals of each species appear to exhibit a range of whorl numbers that fall into a characteristic range). Where whorls were missing for a species, for either reason, all GM-continuous characters for that whorl were coded as missing values. In both cases of breakage and lack of growth, characters were coded as '?' because, though it is possible to represent different types of missing data differently in the matrix, TNT treats all missing data in the same manner.

Traditional characters

In addition to continuous characters based on whorl profile shapes, ten characters previously used in assessing turritellid relationships were included in the matrix (see Allmon, 1996 table 1). Six of these were coded as discrete non-additive characters; (two describing adult lateral sinus shape (figure 2.3), one describing protoconch shape using the definitions of Marwick, 1957a; 1971) and three describing the appearance order of the spiral cords A, B and C (figure 2.3). The remaining four were coded as continuous characters: the number of protoconch whorls, the total number of teleoconch whorls known for each species, the maximum adult shell height, and the maximum adult shell width).

A number of characters that have previously been suggested to be of phylogenetic value, such as spire angle (e.g., see Allmon, 1996), were not used here as they would introduce redundancy into the dataset by duplicating information provided by the geometric morphometric characters.

Phylogenetic analyses

Matrices can be seen in appendices 4 and 5. All analyses were carried out using parsimony in TNT (ver. 1.1; Goloboff et al., 2003a) using the same settings as described for the generic level analysis described above.

The geometric morphometric analyses generated suites of characters in which multiple continuous characters described shape. Each character within one of these suites describes only a portion of the total shape variation, with some of them describing a higher percentage of that shape variation than others. As the continuous characters in a suite are therefore not equal, a number of different weighting schemes were explored in which these morphometric-based characters were weighted differently to reflect this difference in explained shape variation. Four character weighting schemes were explored:

1) All characters weighted equally. The TNT matrix for *Stiracolpus* can be seen in appendix 4 and that of *Zeacolpus* in appendix 5.

2) A "basic weighting" scheme in which all traditional characters were up-weighted to higher weights than the continuous characters, which were left unweighted. In one case ("basic, w=2"), the traditional characters were all weighted at 2 while the GM-

continuous characters were left at 1 producing a much higher combined weight for the GM-continuous characters (336 for the *Stiracolpus* matrix; 420 for the *Zeacolpus* matrix) than the traditional characters (20). In the second case, the traditional characters were upweighted such that their combined weight was slightly higher than that of the GM-continuous characters. For the *Stiracolpus* matrix the traditional characters were weighted to 40 ("basic, w=40"), while for the *Zeacolpus* matrix they were weighted to 44 ("basic, w=44"). Code for these weighting schemes can be found at the end of appendices 4 and 5.

3) An "eigenweighting" scheme. Each continuous character produced from geometric morphometric analysis of whorl profile was weighted to the percentage of variation in the eigenshape analysis described by the axis that generated that character. As with the basic weighting schemes, the traditional characters were upweighted to values greater than that of the maximum weight of the continuous characters. In one case all traditional characters were weighted to a value just higher than that of the maximum eigenweight (in *Stiracolpus* w=20, in *Zeacolpus* w=18) and in the other they were weighted such that the combined weight of the traditional characters was greater than that of the GM-continuous characters (in *Stiracolpus* w=132, in *Zeacolpus* w=171). Code for these weighting schemes can be found at the end of appendices ## and ##.

4) Implied weighting in which the quantity of homoplasy of each character is used to weight them such that the more homoplasious characters are down-weighted more (Goloboff, 1993; Goloboff et al., 2008a). The strength with which characters are weighted is determined by setting a concavity function, k. Lower values of k produce higher weights (e.g., Mirande, 2009; Vega et al., 2009). Various values of k were explored.

Consistency index and retention index were calculated for each phylogeny. Group support was also calculated as group present/contradicted (GC) bootstrap and jackknife values for 1000 replicates (Goloboff et al., 2003b). GC frequencies are not an indication of absolute frequency with which a group occurs in the bootstrap or jackknife bootstrap replicates, but is rather that frequency minus the frequency with which that group is actively contradicted in the replicates. GC bootstrap and jackknife values therefore vary between -100% (complete contradiction) and +100% (complete support) while a value of 0 indicates that the group is equally supported and contradicted (Goloboff et al. describe this as "indifference"). The average frequency of support across the phylogeny (i.e., of all the groups in the bootstrap or jackknife phylogeny) was recorded for each phylogeny, as was the percentage of nodes retained in the bootstrap and jackknife trees. In all of these cases, a higher value indicates better support (Goloboff et al., 2003b).

A frequency difference consensus tree (Goloboff et al., 2008b) was calculated for each genus individually. This takes individual phylogenies calculated by different methodologies, in this case those produced by each weighting scheme, and shows which clades occur in multiple analyses. The percentage of phylogenies in which a group is supported are displayed by each node. Those groupings that occur more frequently are assumed to be better supported (e.g., see Mirande, 2009).

Stratigraphic Indices

In addition to calculating phylogenetic measures of support, two metrics of congruence between phylogeny and stratigraphy were calculated, the Gap Excess

Ratio (GER, Wills, 1999) and the Relative Completeness Index (RCI, Benton and Storrs, 1994).

The Relative Completeness Index is calculated as:

$$RCI = [1-(MIG/SRL)] \times 100$$

While the Gap Excess Ratio is calculated as:

$$GER = 1-(MIG-G_{min})/(G_{max}-G_{min})$$

SRL is the simple range length (i.e., observed range from stratigraphy in years), MIG is the minimum implied gap (i.e., the ghost range: the period of geological time for which a fossil species or lineage is inferred to exist from a phylogeny placed onto a stratigraphic framework but for which no direct fossil evidence is available (Norell, 1992)). G_{min} is the minimum possible amount of ghost range that could occur given the stratigraphic distribution of the species in the analysis under any phylogeny, while G_{max} is the maximum possible ghost range that could occur under any phylogeny. As the outgroup in this analysis is stratigraphically younger than the oldest member of the ingroup, there will always be a ghost range implied for the outgroup and it has not been used in the calculation of the stratigraphic indices used here.

RCI varies from a theoretical maximum of –infinity to +100%; GER varies from 0 to 1. In both cases, larger values indicate better fit of phylogeny to stratigraphy.

Results

The generic level phylogeny can be seen in figure 2.6. It indicates that *Stiracolpus* and *Zeacolpus* do not constitute a monophyletic group as they form part of a large polytomy.

Table 2.2 shows a summary of phylogenetic support statistics and stratigraphic indices for phylogenetic analyses of Stiracolpus and *Zeacolpus* individually. Phylogenies produced for *Stiracolpus* are better supported and show higher stratigraphic congruence than *Zeacolpus* phylogenies. RCI is much lower for all of the *Zeacolpus* analyses than for those of *Stiracolpus* suggesting that the fossil record for *Zeacolpus* is less complete than that of *Stiracolpus* (Wills, 1999).

The best supported phylogeny (i.e., that which had the highest combination of support values) for both *Stiracolpus* and *Zeacolpus*, was under a basic weighting scheme (i.e., GM-continuous characters all weighted to 1 giving a total combined weight from these characters of 336 for the *Stiracolpus* matrix and 420 for the *Zeacolpus* matrix). In both cases, the traditional characters were weighted such that the combination of their weights was a little higher than the total combined weight of the GM continuous characters (i.e., all were weighted at 40 in the *Stiracolpus* matrix and 44 in the *Zeacolpus* matrix).

Implied weighting is intended to reduce disruption due to homoplasy (Goloboff et al., 2008a), but here produced the lowest phylogenetic support statistics in any of the analyses. As k was increased (i.e., strength of weighting decreased), CI and RI values increased for *Zeacolpus* while RCI and GER decreased. For *Stiracolpus*, the pattern is

Figure 2.6: Strict consensus phylogeny produced from seven most parsimonious trees for the genera of the family Turritellidae, generated from characters taken from Allmon, 1996. The Consistency Index is 0.451, the Retention Index is 0.708. *Zeacolpus* and *Stiracolpus* do not form a monophyletic group in this phylogeny as they are part of a large polytomy.

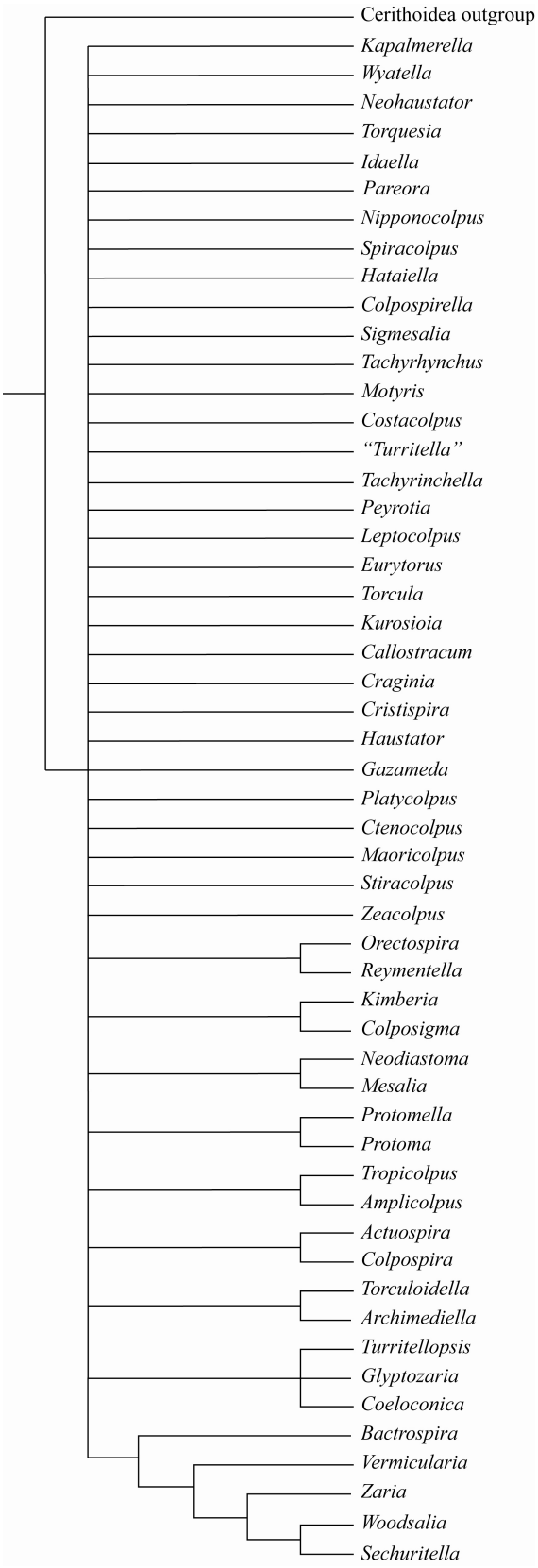

Cerithoidea outgroup
Kapalmerella
Wyatella
Neohaustator
Torquesia
Idaella
Pareora
Nipponocolpus
Spiracolpus
Hataiella
Colpospirella
Sigmesalia
Tachyrhynchus
Motyris
Costacolpus
"Turritella"
Tachyrinchella
Peyrotia
Leptocolpus
Eurytorus
Torcula
Kurosioia
Callostracum
Craginia
Cristispira
Haustator
Gazameda
Platycolpus
Ctenocolpus
Maoricolpus
Stiracolpus
Zeacolpus
Orectospira
Reymentella
Kimberia
Colposigma
Neodiastoma
Mesalia
Protomella
Protoma
Tropicolpus
Amplicolpus
Actuospira
Colpospira
Torculoidella
Archimediella
Turritellopsis
Glyptozaria
Coeloconica
Bactrospira
Vermicularia
Zaria
Woodsalia
Sechuritella

Table 2.2: Phylogenetic support and stratigraphic congruence statistics. Weighting schemes are named as follows: 1) equal weight indicates all characters had an equal weight of 1 in the matrix. 2) implied k=x indicates that implied weighting was used with a k value equal to the value of x. 3) "Basic" indicates all GM-continuous characters were weighted at 1 while all other characters were weighted to the value of w indicated. 4) "Eigenweight" indicates all GM-continuous characters were weighted according to the percentage of variation explained by the eigenaxes while the other characters were all weighted to the value of w. In the second instance of both basic (w=40 or 44) and eigenweight cases(w=132 or 171) $\Sigma w > \Sigma$GM-continuous character weights.

	Weighting scheme	MPT	CI	RI	GC bootstrap	% nodes in BS tree	GC jacknife	% nodes in JK tree	MIG	RCI	GER
Stiracolpus	Equal weighting	169.325	0.487	0.441	21.6	64	21.6	64	59.1	-94.5	0.96
	Implied k=1	50.895	0.435	0.309	7.6	41	8.8	36	57.3	-88.5	0.96
	Implied k=3	21.427	0.424	0.278	9.7	45	11.4	45	43.2	-42.1	0.97
	Implied k=10	7.642	0.462	0.382	10.0	50	12.7	50	49.3	-62.4	0.97
	Basic w=2	222.945	0.525	0.530	21.4	64	21.4	68	59.1	-94.5	0.96
	Basic w=40	2230.614	0.643	0.724	25.3	64	23.6	77	5.5	-95.9	0.96
	Eigenweight w=20	1763.675	0.548	0.589	21.5	77	20.8	68	57.3	-88.7	0.96
	Eigenweight w=132	7682.436	0.631	0.710	24.6	82	23.8	73	60.7	-99.8	0.95
	Frequency Difference phylogeny	-	-	-	-	-	-	-	64.8	-113.4	0.95
Zeacolpus	Equal weighting	133.356	0.644	0.481	7.1	53	6.4	18	329.7	-378.1	0.26
	Implied k=1	31.826	0.557	0.253	7.6	29	7.9	29	241.5	-250.3	0.50
	Implied k=3	12.940	0.606	0.389	6.9	24	4.0	47	278.0	-303.1	0.40
	Implied k=10	4.306	0.644	0.481	6.6	29	6.7	24	287.5	-316.9	0.37
	Basic w=2	1823.673	0.763	0.749	7.7	53	7.7	41	292.7	-324.4	0.36
	Basic w=44	12212.653	0.724	0.720	8.8	65	7.4	41	327.2	-374.5	0.27
	Eigenweight w=18	1351.482	0.671	0.609	7.9	41	7.0	24	323.7	-369.4	0.27
	Eigenweight w=171	8751.527	0.720	0.715	8.5	35	6.0	24	320.4	-364.6	0.28
	Frequency Difference phylogeny	-	-	-	-	-	-	-	317.1	-359.8	0.29

less clear, but CI and RI are higher for k=10 than k=1 while RCI and GER are both higher, but not significantly so. Those phylogenies that had the highest phylogenetic support statistics had the lowest stratigraphic congruence, and vice versa. The frequency difference phylogenies for each genus can be seen in figures 2.7 and 2.8. These both have multiple polytomies, but in both genera there are a number of groupings that emerge as being consistent between the multiple phylogenies they are constructed from.

Discussion

Zeacolpus and *Stiracolpus* are supported here as being separate, monophyletic groups rather than a genus and subgenus. This is contrary to Marwick's (1957a; 1957n; 1971b) classification of the two as a genus (*Zeacolpus*) and sub-genus (*Zeacolpus* (*Stiracolpus*)). The phylogenetic hypotheses generated for both genera indicate significant ghost ranges

(c.f., Norell, 1992; Paul, 2004), see figures 2.9 and 2.10. While these are quite large, they are within the range of ghost ranges seen throughout the fossil record (see Wills, 2007 and references therein.)

The placement of the stratigraphically oldest of the *Zeacolpus* species, *Z. gagei*, is responsible for much of the ghost range elongations seen in the *Zeacolpus* phylogeny (figure 2.10). The ghost range is the period of time between the origination of a species as implied by the phylogeny and its first appearance in the fossil record. Therefore, if the stratigraphically oldest of the species in the analysis does not occur at

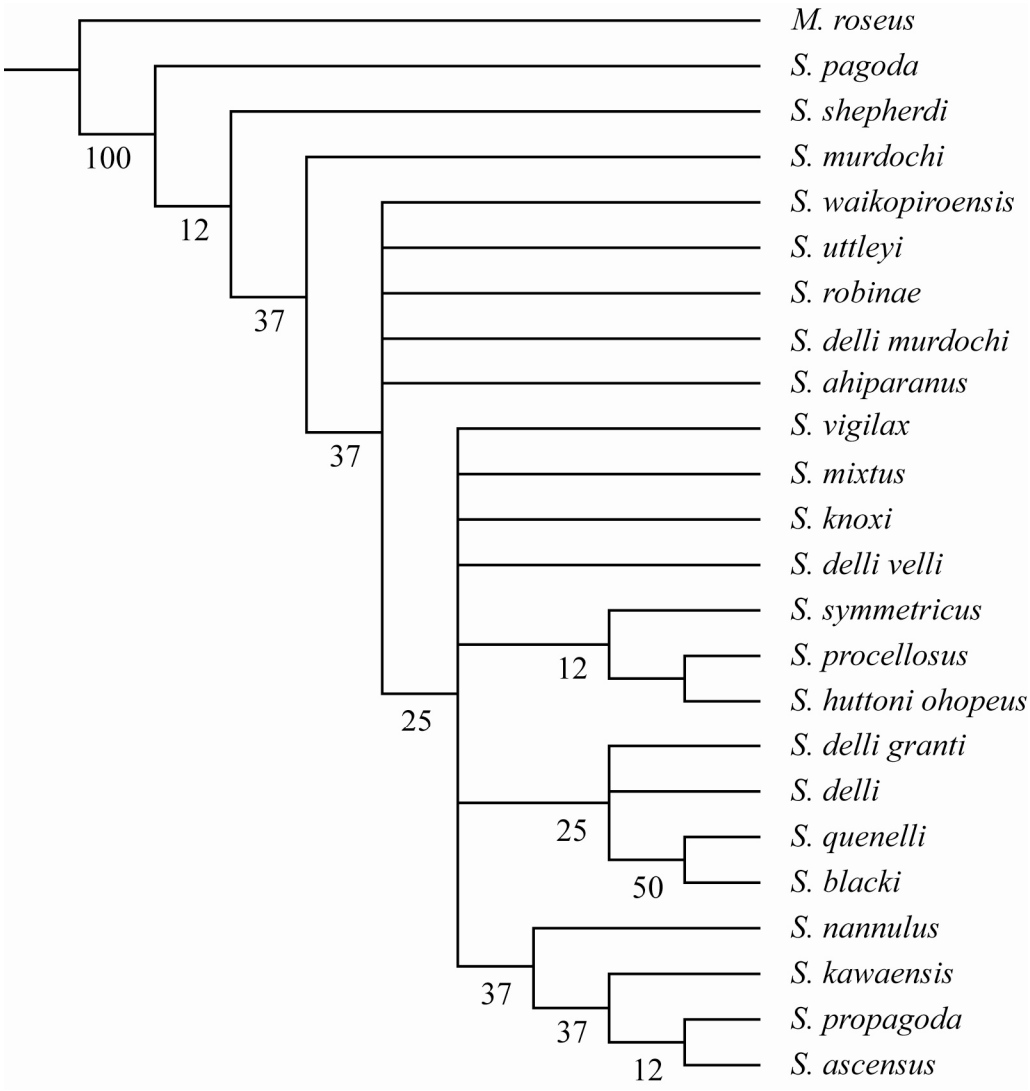


Figure 2.7: *Stiracolpus* frequency difference consensus generated using phylogenies calculated under the four different weighting schemes described. Groupings and relationships present in multiple phylogenies are show here with numerical values indicating the percentage of phylogenies they occur in. Polytomies occur where clades are consistent but the relationships within them are not.

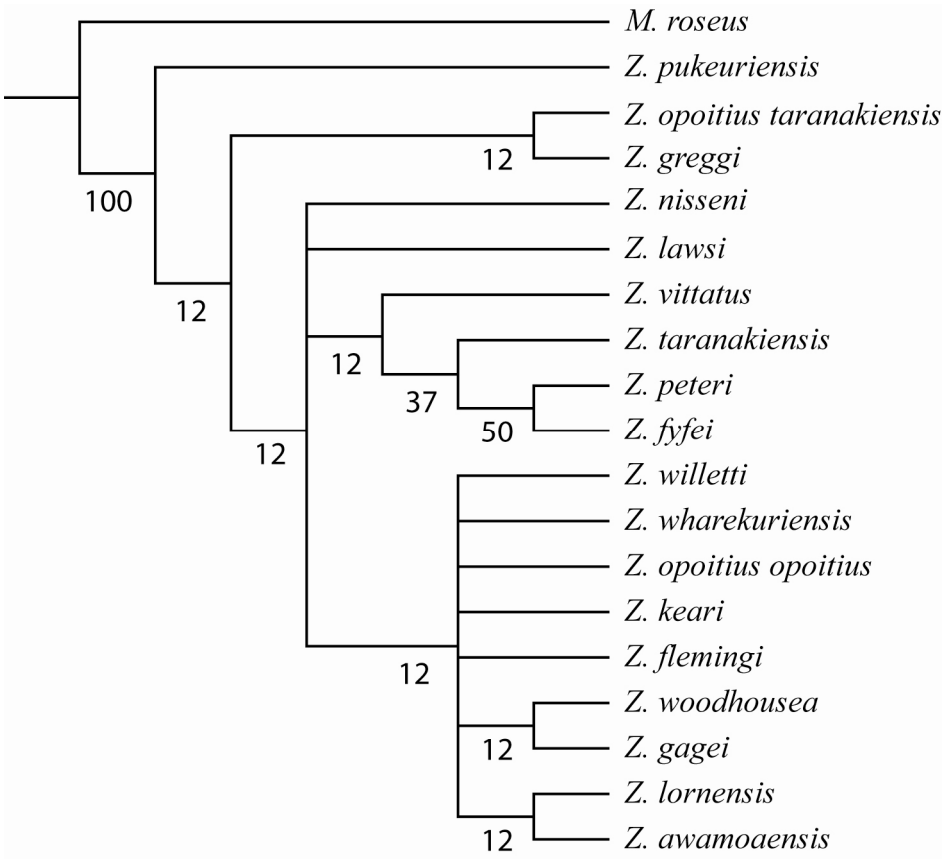


Figure 2.8: *Zeacolpus* frequency difference consensus generated using phylogenies calculated under the four different weighting schemes described. Groupings and relationships present in multiple phylogenies are show here with numerical values indicating the percentage of phylogenies they occur in. Polytomies occur where clades are consistent but the relationships within them are not.

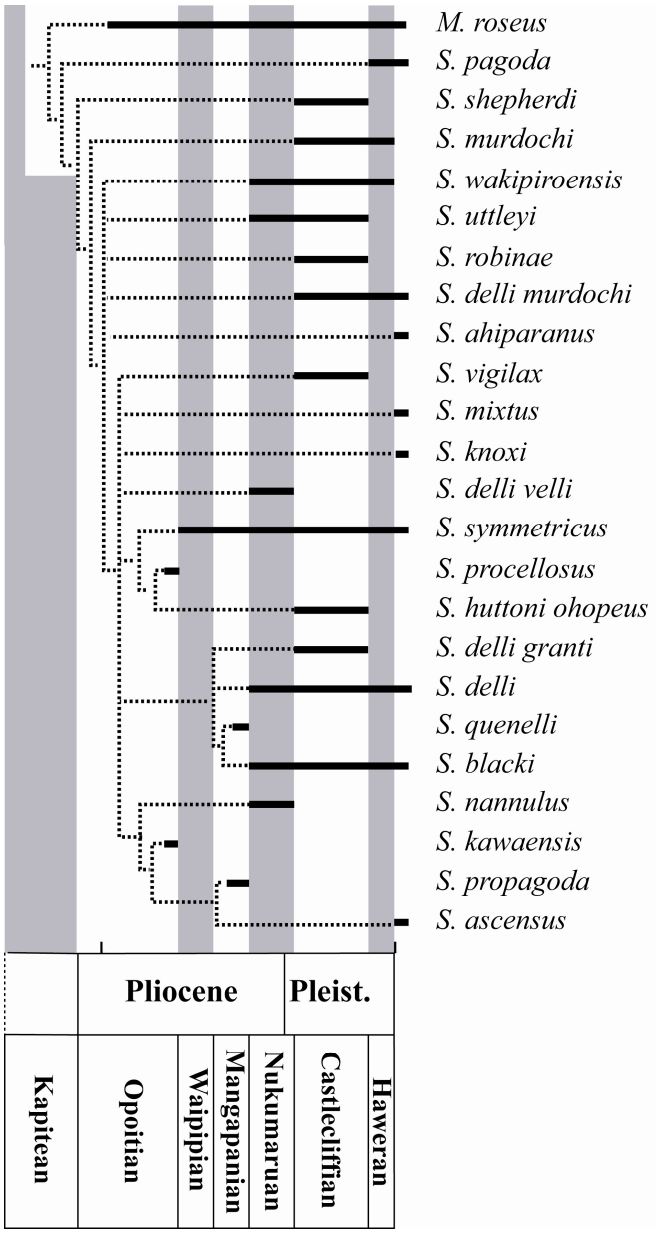
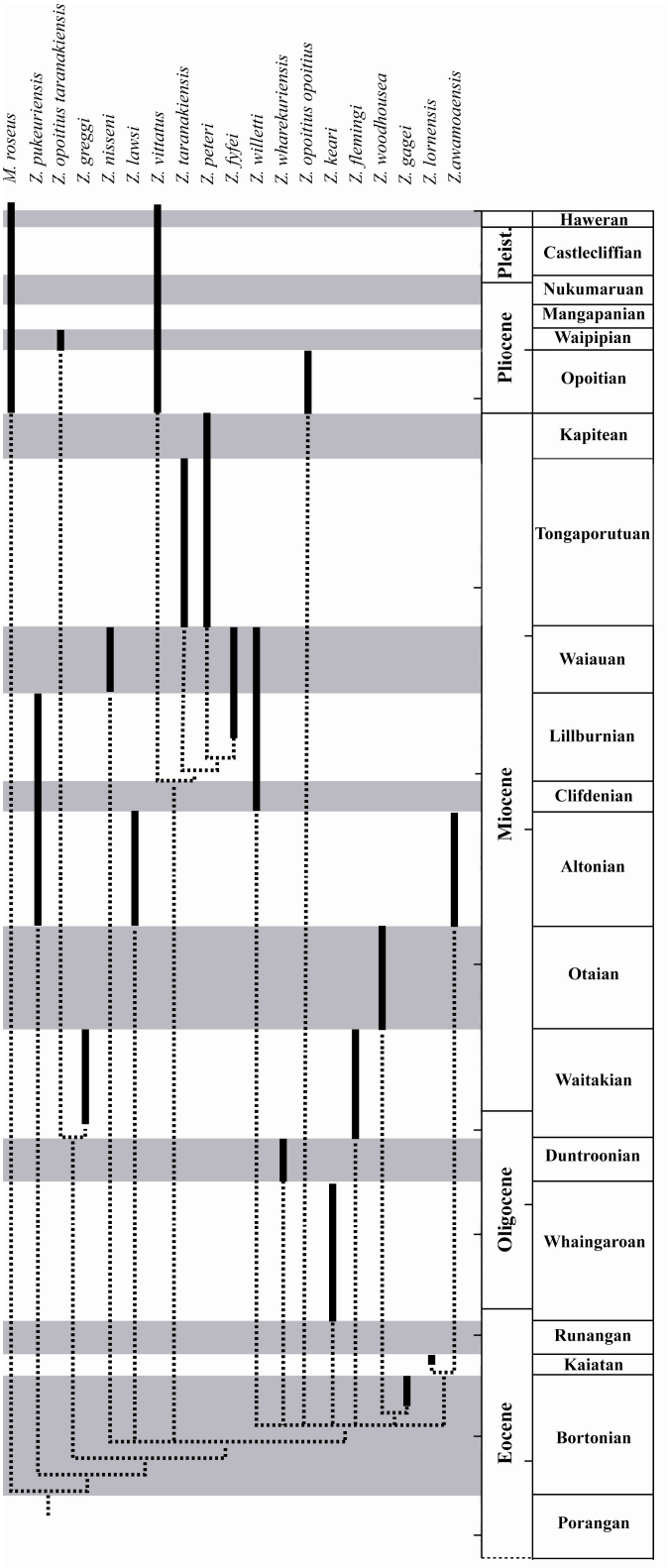


Figure 2.9: Ghost ranges of *Stiracolpus* implied by frequency difference consensus (figure 2.7). Solid black lines indicate the stages from which a species has been reported but do not necessarily imply that species is present throughout the entire stage. Dotted lines indicate implied ghost range inferred from phylogeny. Species ranges have occasionally been shortened to not range through an entire stage in order to accommodate branching events inferred to occur within that stage. Such "shortened" ranges do not imply that species occurred only in the later part of that stage

Figure 2.10: Ghost ranges of *Zeacolpus* implied by frequency difference consensus (figure 2.8). Solid black lines indicate the stages from which a species has been reported but do not necessarily imply that species is present throughout the entire stage. Dotted lines indicate implied ghost range inferred from phylogeny. Species ranges have occasionally been shortened to not range through an entire stage in order to accommodate branching events inferred to occur within that stage. Such "shortened" ranges do not imply that species occurred only in the later part of that stage


M. roseus
Z. pukeuriensis
Z. opoitius taranakiensis
Z. greggi
Z. nisseni
Z. lawsi
Z. vittatus
Z. taranakiensis
Z. peteri
Z. fyfei
Z. willetti
Z. wharekuriensis
Z. opoitius opoitius
Z. keari
Z. flemingi
Z. woodhousea
Z. gagei
Z. lornensis
Z.awamoaensis
Haweran
Pleist.
Castlecliffian
Nukumaruan
Mangapanian
Pliocene
Waipipian
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Miocene
Altonian
Otaian
Waitakian
Duntroonian
Oligocene
Whaingaroan
Runangan
Kaiatan
Eocene
Bortonian
Porangan

the base of the phylogeny other species will automatically have a ghost range associated with them.

The completeness of the fossil record of *Zeacolpus* appears to be lower than that of *Stiracolpus* based on the congruence of phylogeny and stratigraphy. This may be at least in part due to the stratigraphic distribution of the two genera. *Stiracolpus* occurs in the approximately continuous unlithified shallow shelf strata of the Pliocene and Pleistocene

(Naish, 2005; Crampton et al., 2006b; Hendy, 2009) whereas *Zeacolpus* is largely pre-Pliocene occurring through periods in which turritellids have a much lower preservation potential due to decreased shelf facies being sampled, poor outcrop area and poor sampling of some stages (see Crampton et al., 2003; 2006a). The ghost ranges implied for *Stiracolpus* are therefore more surprising given the high completeness of the major Plio-Pleistocene basins (e.g., Naish et al., 1998). However, despite the local high completeness of basins such as the Wanganui and Taranaki basins, there were other basins that are not preserved now in which turritellid species would also have been living. Some species (e.g., *S. kawaensis*) are only known from less extensive outcrop localities elsewhere in New Zealand outside of known basins with extensive outcrop area. Beu (2004) noted that multiple periods of migration between the northern parts of New Zealand and the more southern basins that are currently geographically isolated has occurred repeatedly through at least the last 2My as sea-level has varied. Some *Stiracolpus* species have likely been able to do the same, immigrating into the more stratigraphically complete areas after originating elsewhere in New Zealand.

Much of the Middle Miocene of New Zealand is represented by deep-water bathyl deposits (e.g., see Crampton et al., 2003), rather than shallow-water shelf faunas such as those seen in the Pliocene and Pleistocene rocks in which turritellids are more likely to be found. There are also periods of very low outcrop area throughout the Eocene to Miocene (Beu, 1990; Crampton et al., 2006a). Additionally, a large portion of the Miocene deposits in New Zealand are the results of sequences developing in isolated basins (Beu and Maxwell, 1990; Cooper, 2004), making it possible that species are limited in their stratigraphic occurrence by their geographic distribution.

For both *Stiracolpus* and *Zeacolpus*, Marwick posited stocks (lineages) changing through time. In *Stiracolpus*, (see Marwick, 1957a figure 5), he even suggested possible hybridizations between species producing intermediate forms. This suggested set of relationships assumed anagenetic change in lineages through time and is based on a combination of stratigraphic occurrence and variation in morphology, (largely strength of expression of ornament through ontogeny). In the case of *Zeacolpus* Marwick (1971) suggested lineages of species, largely based on stratigraphic occurrence information. He made no attempt to suggest interbreeding between species of *Zeacolpus*, perhaps because of the far fewer instances of multiple species occurring in a stage. In this study, all species are treated as terminal taxa in the phylogenetic analysis rather than as a series of ancestors and descendants so it is perhaps unsurprising that the hypothesis of relationships here are not very similar to those Marwick suggested.

Marwick described a number of sub species, such as the numerous sub species of *Stiracolpus delli*. However, of the three sub species described, only one occurs as a sister species of *S. delli*; the others all occur in different parts of the phylogeny. This

suggests that with the exception of *S. dell granti*, the sub species of *S. delli* described by Marwick, 1957 should be assigned to species level. In the *Zeacolpus* analyses, the two sub species of *Z. opoitius* described by Fleming, 1966 do not occur as sister taxa, again suggesting that their taxonomic level should be revised.

The generation of whorl profile shape using geometric morphometric methods does appear to have some utility in the phylogenetic analysis of turritellid shell shape, though it should be applied cautiously. In addition to whorl shape, there are other features of the shell that may also be amenable to description in a similar way. For instance, the sinus shape can also be described as a simple curve which would be amenable to eigenshape analysis.

Conclusions

This study suggests that *Zeacolpus* and *Stiracolpus* are individual genera. Ghost ranging is prevalent in both genera, something that is a function of the stratigraphy of the rocks in which these species are found. Ghost ranges are more extensive in *Zeacolpus* partly due to the nature of the stratigraphy of the pre-Pliocene rock record of New Zealand.

The phylogenetic relationships described here for *Stiracolpus* are not very similar to those relationships proposed by Marwick based on gross morphology and stratigraphic occurrences. Similarly, the *Zeacolpus* relationships here do not align closely with the "lineages" Marwick proposed. Additionally, many of the sub species described by Marwick and Fleming require reassignment to species level to reflect the phylogenetic relationships suggested here.

Given previous difficulties in constructing robust phylogenies for turritellid gastropods, continuous character data generated from eigenshape analysis of whorl profile shape does appear to have some utility in generating phylogenetic hypotheses in conjunction with traditional characters. This opens up the possibility of phylogenetic analysis of other turritellid groups around the world. As turritellids have such potential for use in macroevolutionary studies given their fossil record and morphology etc. the ability to generate phylogenetic hypotheses will be extremely useful. As turritellids have such potential for use in macroevolutionary studies given their fossil record and morphology etc. the ability to generate phylogenetic hypotheses will be extremely useful. This is not limited to turritellid gastropods. The use of geometric morphometric methodologies to generate phylogenetic characters should be more widely applicable, opening up the possibility of generating phylogenies for many taxa that have previously proved intractable to phylogenetic analysis using traditional characters.

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CHAPTER 3

MACROEVOLUTIONARY PATTERNS IN THE CENOZOIC NEW ZEALAND TURRITELLID GENERA *ZEACOLPUS* AND *STIRACOLPUS* (GASTROPODA: TURRITELLIDAE)

Abstract

First appearance datums (FADs) in the New Zealand Cenozoic molluscan record have a long history of use in a variety of studies. The distributions of raw FADs of the turritellid gastropods largely conform to the pattern seen in the rest of the fauna. When, these FADs are corrected to account for phylogenetic relationships of the species, however, the pattern of originations is significantly different. Rather than showing approximately constant origination rates from the first appearance of *Zeacolpus*, originations are clustered into four periods; in the Middle Eocene, Late Oligocene/Early Miocene, late Middle Miocene and the Pliocene. Cooling climatic conditions are associated with most of these peaks of origination but in the older Cenozoic strata sampling biases obscure this correlation. In the Pliocene, the association is better constrained, but a full correlation of species occurrences with the detailed sequence stratigraphy of the Pliocene and Pleistocene has not yet been carried out to further test this hypothesis. With the exception of a few lineages, *Zeacolpus* was a more warm-water taxon than *Stiracolpus* which radiated in the Pliocene where *Zeacolpus* did not. The majority of species in other New Zealand turritellid genera also appear to be warmer-water taxa, reinforcing previous observations that modern turritellids do not share the same environmental tolerances as their earlier Cenozoic relatives.

Introduction

To investigate speciation in the fossil record it is necessary to know when new species actually first occur. One way to assess this is to use counts of first appearance datums (FADs, i.e., where a taxon first appears in the stratigraphic record), and many studies have used such FAD counts to examine macroevolutionary patterns and make inferences about causation (for instance, Sepkoski, 1978; 1979; 1984; Jackson and Johnson, 2000; Kirchner and Weil, 2000; Allmon, 2003; Foote, 2005; Brett et al., 2007; Foote, 2007; Alroy, 2008; Alroy et al., 2008). Because of the incompleteness of the fossil record, however, almost all first appearance datums (FADs, i.e., where a taxon first appears in the stratigraphic record) will be later than the actual first appearance of a taxon (Schoch, 1989).

The interval between actual origination and the FAD will vary from taxon to taxon and is unpredictable without knowledge of the phylogenetic relationships of that taxon, though it has generally been assumed to be small (e.g., Schoch, 1989). A "ghost range" (Norell, 1992; Benton, 1994, see also Norell and Novacek, 1992; Benton and Storrs, 1994; Paul, 2004), is the gap between actual origination and a taxon's appearance in the stratigraphic record. These can be inferred where phylogeny and stratigraphy are not completely congruent and sister taxa that should have originated at the same time appear to originate at different times. A ghost range is inferred to occur from the time of actual origination implied by a phylogeny to the time at which the taxon is first seen in the stratigraphic record. A phylogeny is therefore required to calculate ghost ranges and recognize an implied first origination time older than the FAD. These implied originations may indicate a significantly different pattern of evolution than "raw" FAD data.

To study patterns of speciation in the fossil record, a group with an excellent fossil record and a known phylogeny is needed. The turritellid gastropods of New Zealand may provide such a system. In this chapter, phylogenies of the turritellid genera *Zeacolpus* and *Stiracolpus* (see chapter 2) are used to calculate actual first appearances in order to examine their speciation patterns through the Cenozoic, and attempt to identify possible causes for the observed patterns.

The New Zealand Cenozoic mollusk record is one of the most abundant, diverse, and well studied in the world. There has been extensive taxonomic work on these mollusk faunas (e.g., Marwick, 1929; Laws, 1934a; 1934b; 1940; Fleming, 1955; Beu, 1970; Maxwell, 1978; Beu and Maxwell, 1990; Maxwell, 1992; Stillwell, 1993; Beu, 2004; Beu, 2006), and they have been used extensively in biostratigraphy (e.g., Beu, 1969; Cooper et al., 2001; Cooper, 2004) and paleoenvironmental reconstruction (e.g., Fleming, 1944; Beu, 1974). The mollusk record of New Zealand has also been used in a series of detailed examinations of diversity patterns (e.g., Beu, 1990; Crampton et al., 2003; Crampton et al., 2006b; Hendy, 2007; Hendy et al., 2009) that have examined potential biases in the record.

The Pliocene and Pleistocene basins of New Zealand contain some of the most complete stratigraphic records of this time interval in the world. They consist of stacked series of cyclic shallow-marine strata providing what is, apart from unconformities that form parts of the cyclothem sequences, a relatively continuous sedimentary sequence through most of the Pliocene and Pleistocene: only small time periods are missing due to lack of exposures (e.g., see Naish et al., 1998; Saul et al., 1999). These strata are well exposed on land due to upwarping along the boundary of

the Pacific and Australian plates (Naish, 2005). When Fleming (1953) described the fossiliferous sections of the Wanganui Basin, he recognized that up to 35 sea-level fluctuations were visible in the basin. Since then, an enormous amount of work has been carried out in the Wanganui and other basins (e.g., Vella, 1963; Beu and Edwards, 1984; Kamp and Turner, 1990; Abbott and Carter, 1994; Abbott and Carter, 1999; Pillans et al., 1994; Naish et al., 1998; Saul et al., 1999; Abbott et al., 2005; Naish et al., 2005b; Naish et al., 2005a; Turner et al., 2005), which has provided an extremely high resolution and well understood chrono-stratigraphic framework for the late Pliocene and Pleistocene of New Zealand.

Turritellid gastropods (Cerithioidea, Turritellidae) are an important component of the New Zealand Cenozoic fossil mollusk record (e.g., Marwick, 1957a; 1957b; 1971). They are widely distributed geographically and occur throughout the Cenozoic. There are nine genera, five of which are represented by multiple species, which are often useful for biostratigraphy (e.g., Beu and Maxwell, 1990; Cooper, 2004). In addition, there are a number of modern species representing three of these genera (*Zeacolpus*, *Stiracolpus* and *Maoricolpus*), living around the coast of New Zealand today. All three of these genera are well represented in the fossil record by multiple species. As with turritellids of other geographic regions, fossil and recent turritellids are often found in high abundances (e.g., Allmon, 2007) and are ecologically very important components of the faunas in which they are found.

Patterns seen in the New Zealand mollusk record

For the New Zealand Cenozoic, three intervals of high concentrations of first appearances in mollusk species have long been observed (e.g., Beu, 1990; Beu and

Maxwell, 1990). The two major peaks occur in the Bortonian (equivalent to the end of the Lutetian and start of the Bartonian ages of the late Middle Eocene; see figure 3.1) and the Duntroonian (approximately equivalent to the Middle Chattian age of the Late Oligocene; see figure 3.1). In combination these account for approximately 25% of first appearances of molluscan genera through the entire Cenozoic (calculated from range data in Beu and Maxwell, 1990). These peaks do not coincide with peaks of maximum recorded diversity (Beu, 1990; Crampton et al., 2006b; Hendy, 2007).

Raw FAD patterns for all New Zealand turritellid species based on species range charts from Beu and Maxwell, 1990 (see figure 3.2a) show an approximately continuous background of appearances, although there is a gap after their first appearance in the Paleocene (*Leptocolpus semiconcavus*) until all other genera appear in the Middle Eocene Bortonian stage. Amongst this background of first appearances, there are several peaks, notably a peak in the Middle Oligocene to Middle Miocene, and high numbers of first appearances at the base of the Pliocene, the last stage of the Pliocene, and the base of the Pleistocene.

A more conservative assessment of occurrence counts can be made by counting the minimum number of possible cladogenetic events. This is done by counting first appearances in a stage only when there are more species in that stage than in the previous, e.g., if there are five species in stage “a” and eight in stage “b”, the minimum number of cladogenetic events is counted as three on the assumption that

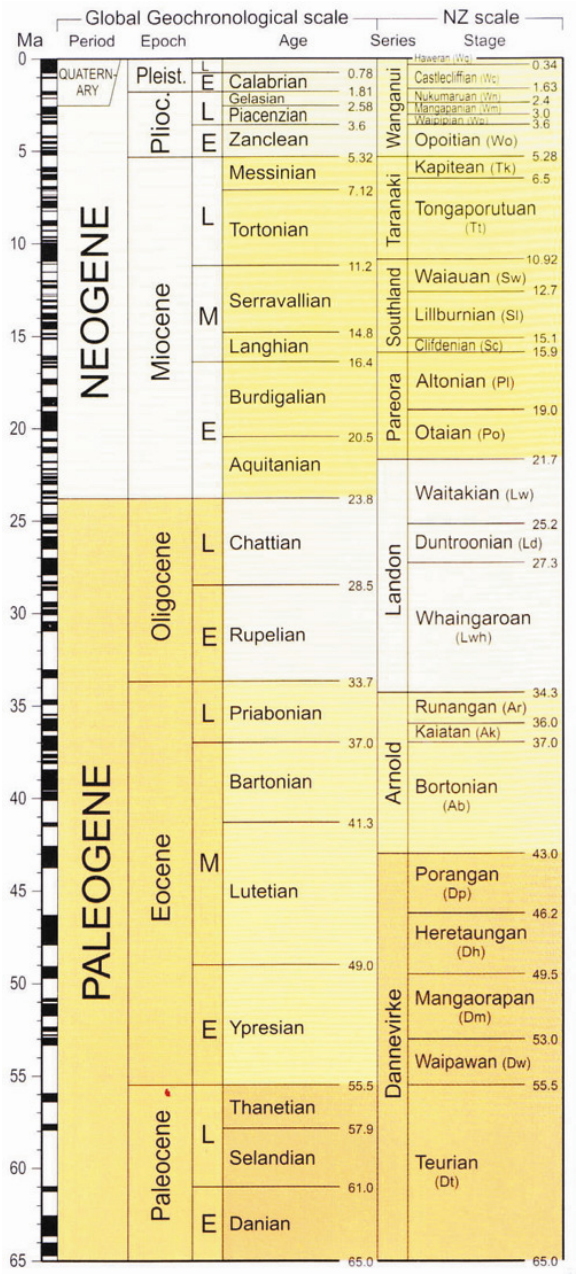


Figure 3.1: Extract of the New Zealand Geological Timescale (Cooper, 2004) showing the Cenozoic. Correlation of the New Zealand stages with International age names.

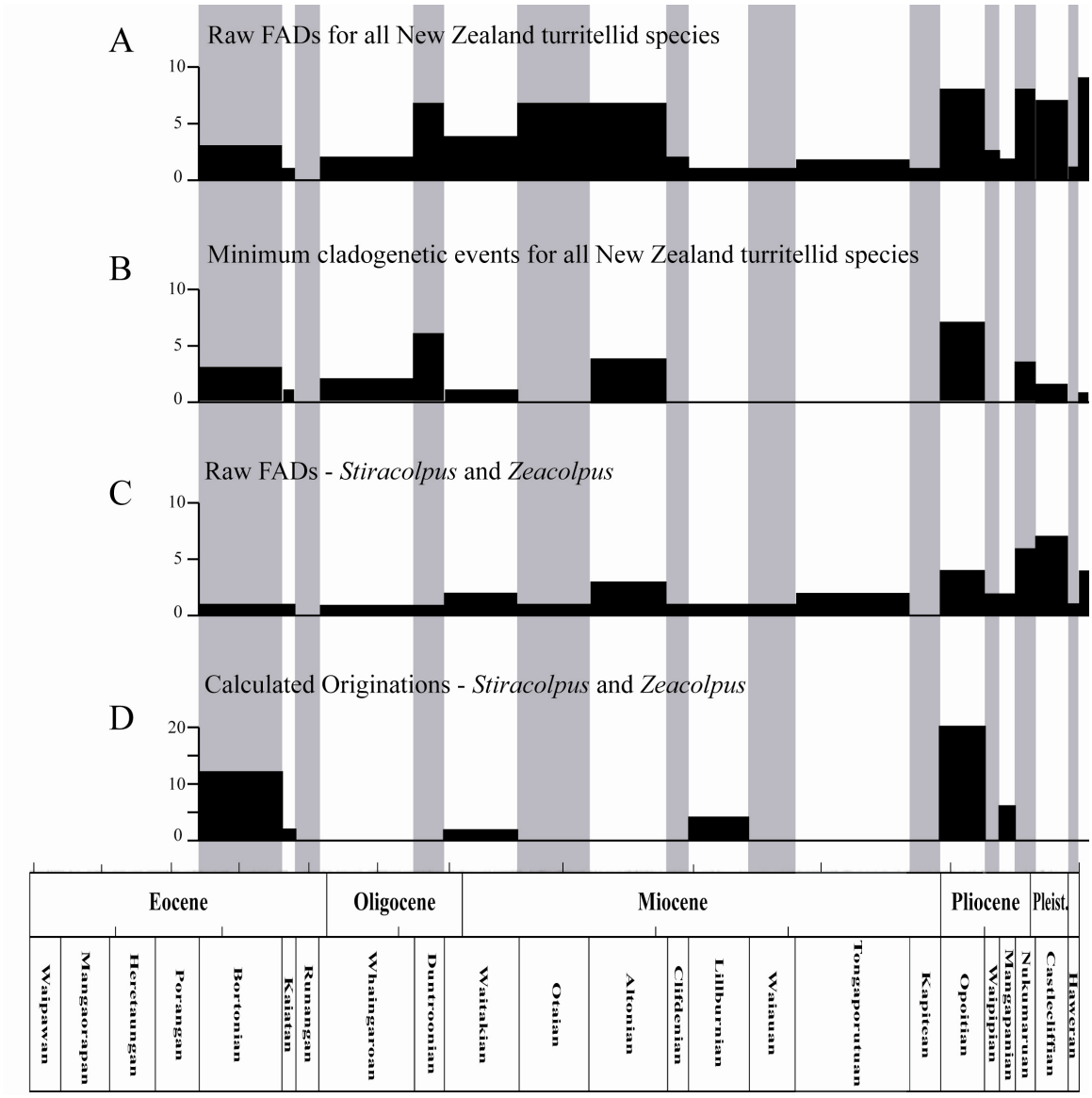


Figure 3.2: A) Raw first appearance data for all New Zealand turritellid species, B) Minimum cladogenetic events for all New Zealand turritellid species, C) Raw FADs for *Stiracolpus* and *Zeacolpus*, D) Calculated FADs for *Stiracolpus* and *Zeacolpus* based on the ghost ranges calculated from the phylogenetic relationships shown in figures 3.3 and 3.4.

five of the species in stage “b” could be taxa that range through from stage “a” to “b” under a different name. When the minimum number of cladogenetic events is calculated for the New Zealand turritellids, the pattern is different from that of the raw FAD data (figure 3.2b); the peaks seen in the raw counts diminish but remain present, whereas the “background” FADs disappear.

The raw data and the minimum possible cladogenetic events do not take into account the phylogenetic history of the species, which can be used to estimate ghost ranges. When this is accounted for, the potential ghost range of each species can be seen. The minimum possible first appearance implied by the phylogeny is where the species splits from its sister group. The actual first occurrence of the species may of course still be earlier than this minimum implied first appearance. In both genera the ghost ranges implied by the phylogenies are quite long (see figures 3.3 and 3.4), but are not unusually so for marine invertebrates (e.g., see Wills, 2007 and references therein). The longest ghost range implied in *Zeacolpus* is around 35My, suggesting either that long periods of stasis have occurred or that some anagenetic change has been involved in some of these lineages. Without better sampling resolution, however, this is impossible to resolve.

For the two genera *Zeacolpus* and *Stiracolpus*, the raw FAD values appear similar to the pattern of all New Zealand turritellids, showing approximately even distribution of appearances from the Bortonian onwards, with an increase in the Pliocene and Pleistocene (figure 3.2c). However, once phylogenetic relationships are taken into account and ghost ranges calculated (figures 3.3 and 3.4), to find the minimum time of first occurrence (i.e., the minimum implied first appearance), the pattern changes to

Figure 3.3: Ghost ranges of *Stiracolpus* implied by frequency difference consensus phylogeny calculated from input phylogenies generated by a number of different weighting schemes using continuous characters from geometric morphometric methods (chapter 2). Solid black lines indicate the stages from which a species has been reported but do not necessarily imply that species is present throughout the entire stage. Dotted lines indicate implied ghost range inferred from phylogeny. Species ranges have occasionally been shortened to not range through an entire stage in order to accommodate branching events inferred to occur within that stage. Such "shortened" ranges do not imply that species occurred only in the later part of that stage

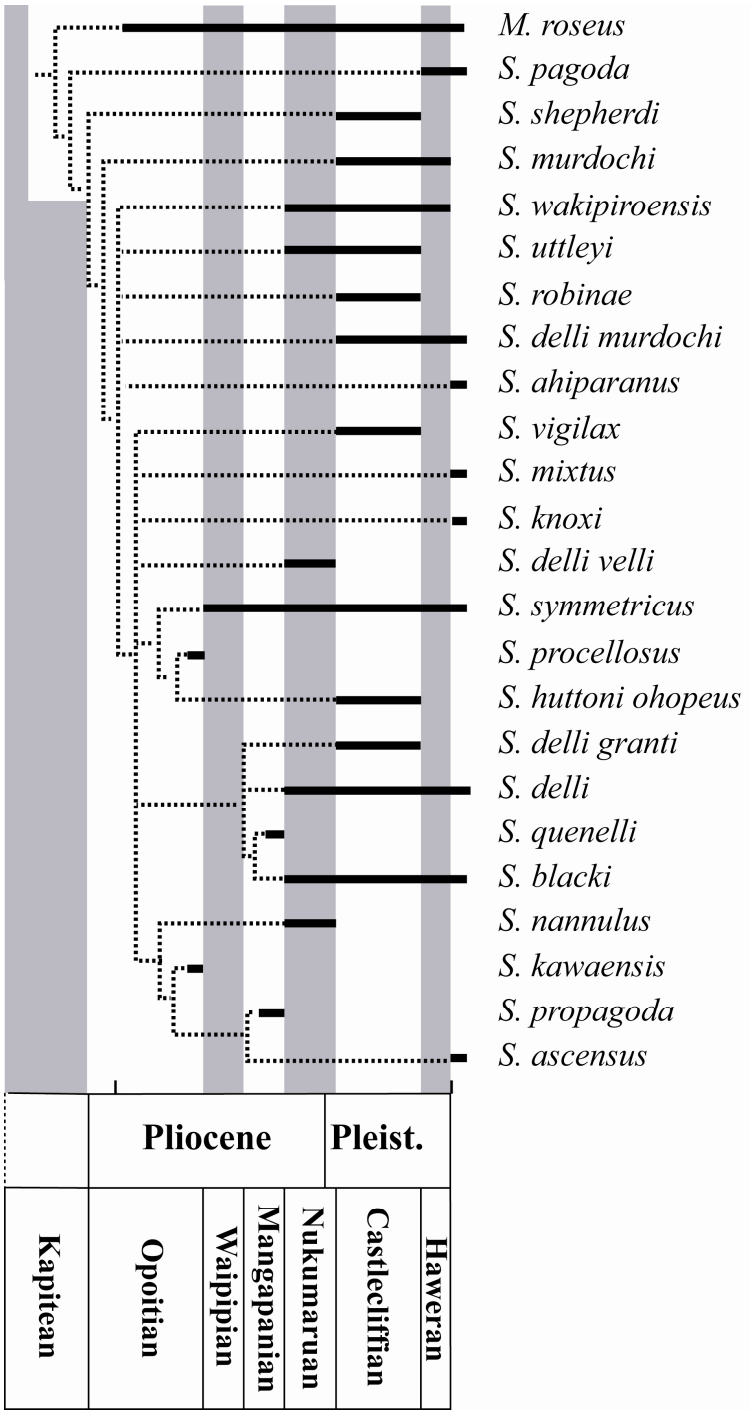
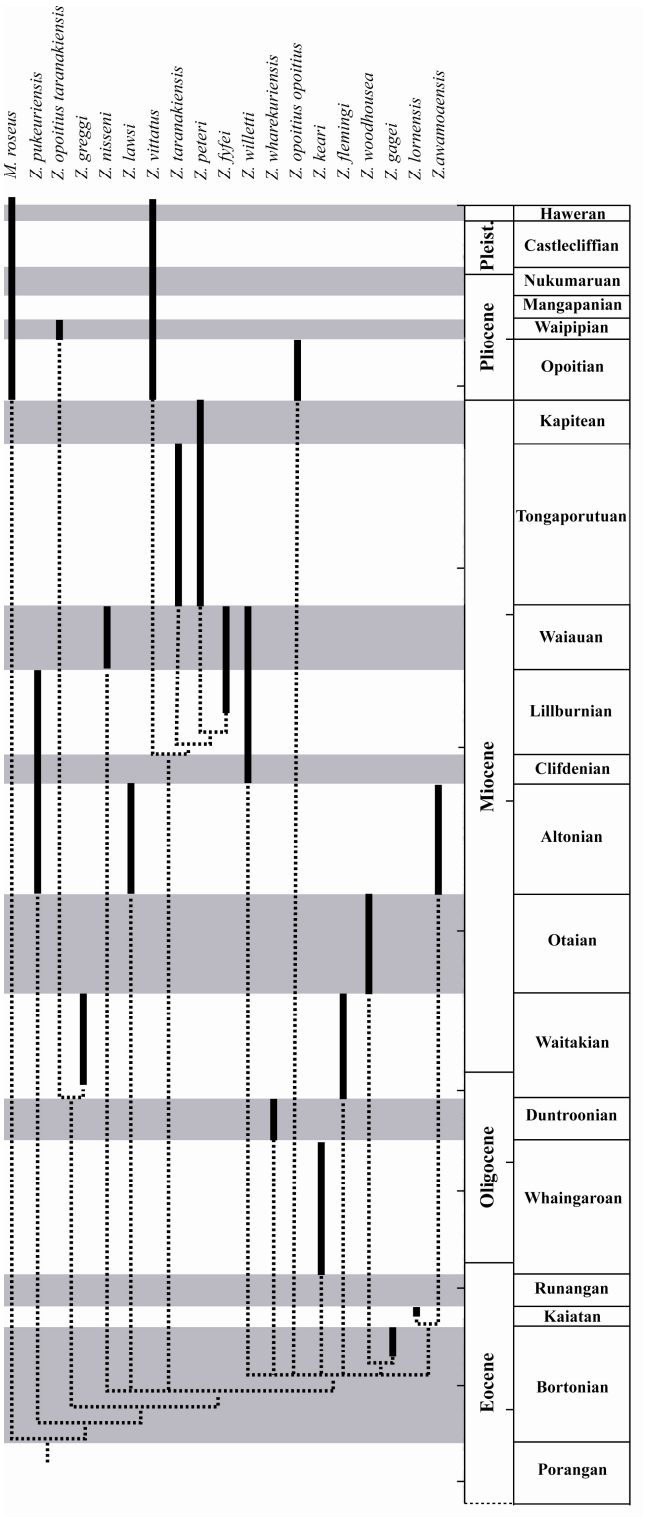

M. roseus
S. pagoda
S. shepherdi
S. murdochi
S. wakipiroensis
S. uttleyi
S. robinae
S. delli murdochi
S. ahiparanus
S. vigilax
S. mixtus
S. knoxi
S. delli velli
S. symmetricus
S. procellosus
S. huttoni ohopeus
S. delli granti
S. delli
S. quenelli
S. blacki
S. nannulus
S. kawaensis
S. propagoda
S. ascensus
Pliocene
Pleist.
Kapitean
Opoitian
Waipipian
Mangapanian
Nukumaruan
Castlecliffian
Haweran

Figure 3.4: Ghost ranges of *Zeacolpus* implied by frequency difference consensus phylogeny calculated from input phylogenies generated by a number of different weighting schemes using continuous characters from geometric morphometric methods (chapter 2). Solid black lines indicate the stages from which a species has been reported but do not necessarily imply that species is present throughout the entire stage. Dotted lines indicate implied ghost range inferred from phylogeny. Species ranges have occasionally been shortened to not range through an entire stage in order to accommodate branching events inferred to occur within that stage. Such "shortened" ranges do not imply that species occurred only in the later part of that stage


M. roseus
Z. pukeuriensis
Z. opoitius taranakiensis
Z. greggi
Z. nisseni
Z. lawsi
Z. vittatus
Z. taranakiensis
Z. peteri
Z. fyfei
Z. willetti
Z. wharekuriensis
Z. opoitius opoitius
Z. keari
Z. flemingi
Z. woodhousea
Z. gagei
Z. lornensis
Z.awamoaensis
Haweran
Pleist.
Castlecliffian
Nukumaruan
Mangapanian
Waipipian
Pliocene
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Miocene
Altonian
Otaian
Waitakian
Duntroonian
Oligocene
Whaingaroan
Runangan
Kaiatan
Eocene
Bortonian
Porangan

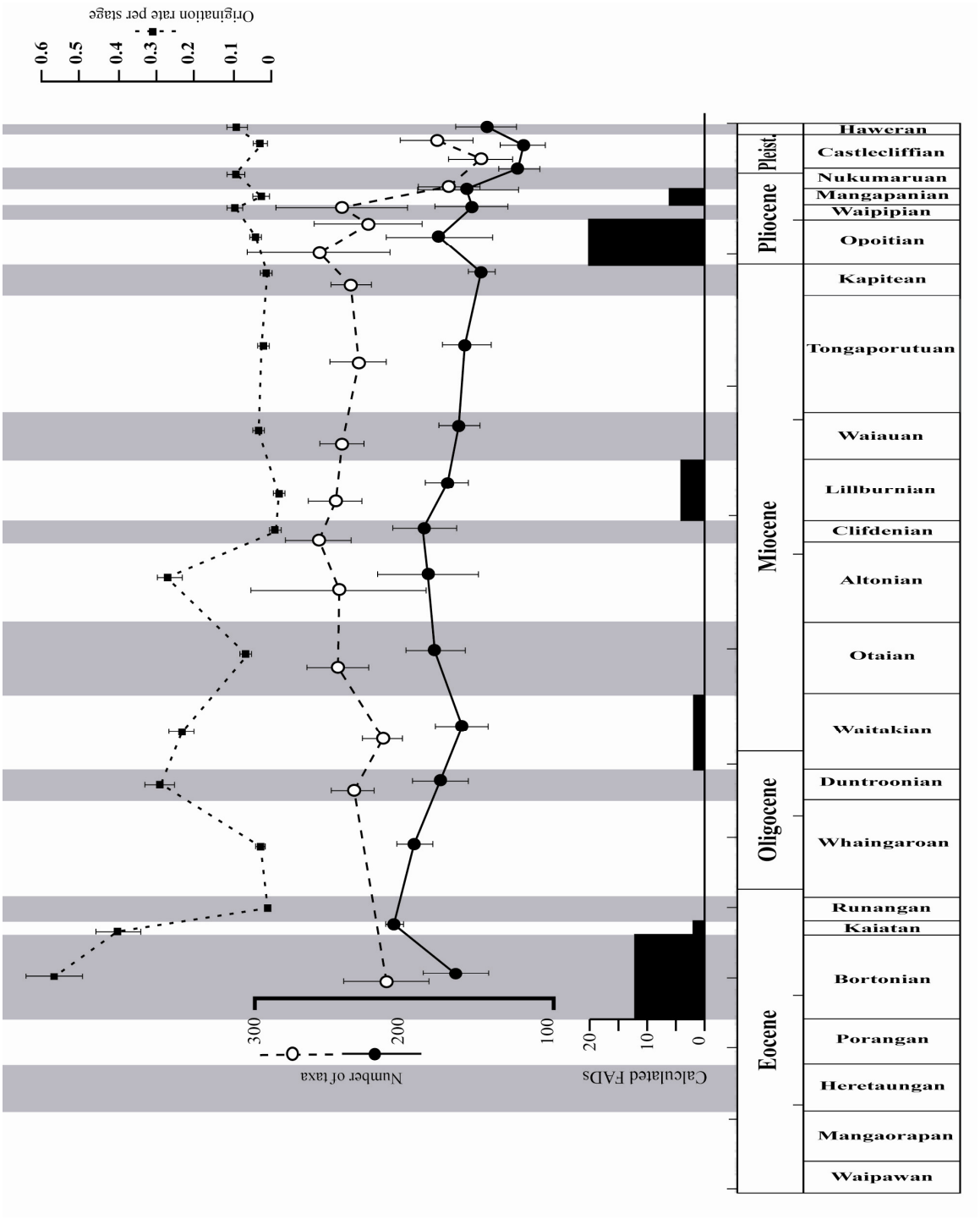
show all implied first appearances being split into four groups: a Middle Eocene peak (Bortonian/Kaiatan), a small late Oligocene/Early Miocene peak (Waitakian), a Middle Miocene peak (Lillburnian) and two peaks in the Pliocene (Opoitian and Mangapanian) (figure 3.2d).

This calculated pattern for *Zeacolpus* and *Stiracolpus* largely conforms to the reported periods of maximal first appearance in the New Zealand Cenozoic mollusks as a whole. What is not seen in these calculated implied FADs is a peak in first appearances, in the Otaian-Altonian stages (Early Miocene), when a number of warm-water taxa apparently moved into New Zealand during the Miocene Thermal Maximum (Beu, 1990). There is, however, a peak in implied FADs the Lillburnian (shortly after the Altonian).

Crampton et al. (2006b) calculated origination rates for all New Zealand fossil mollusks based on their standardized diversity curves for the Cenozoic (see figure 3.5). These rates largely coincide with previous observations (e.g., Beu, 1990), showing peaks in the Late Eocene, Late Oligocene and Middle Miocene. The peak in *Zeacolpus* originations seen here in the Lillburnian (figures 3.2 and 3.4) does not correspond with any previously reported peak in the rest of the molluscan fauna, and in fact corresponds with the period of minimum origination rate from Crampton et al.'s data.

Several studies have suggested a major extinction of New Zealand mollusks at the end of the Miocene (Beu, 1990; Crampton et al., 2003; Crampton et al., 2006b), followed by a major increase in diversity in the Early Pliocene. More recent work, however (Hendy et al., 2009), suggests that this decrease in diversity at the end of the Miocene in the Kapitean stage may be, at least in part, an artifact of facies preservation. Hendy

Figure 3.5: Origination rate and diversity curves adapted from Crampton et al., 2006 shown with calculated originations based on phylogenetic relationships of the two genera *Stiracolpus* and *Zeacolpus*. The peak in the Bortonian and Opoitian correspond to periods of high origination in the rest of the New Zealand molluscan fauna. The peak in *Zeacolpus* originations in the Lillburnian and that of *Stiracolpus* in the Mangapanian seen here correspond to periods of minimal origination rate in the rest of the molluscan fauna.


Origination rate per stage
0.6
0.5
0.4
0.3
0.2
0.1
0
Number of taxa
300
200
100
Calculated FADs
20
10
0
Haweran
Castlecliffian
Nukumaruan
Mangapanian
Waipipian
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Altonian
Otaian
Waitakian
Duntroonian
Whaingaroan
Runangan
Kaiatan
Bortonian
Porangan
Heretaungan
Mangaorapan
Waipawan
Pleist.
Pliocene
Miocene
Oligocene
Eocene

et al.'s study examined variations in sampling intensity between stages and suggested that the apparent rapid increase in diversity through the Pliocene and Pleistocene is also partly due to increasing preservation of nearshore faunas and therefore increased sampling of diverse molluscan faunas (see also Crampton et al., 2006a).

Instead, Hendy et al., argue that the Mio-Pliocene decline and rebound were much smaller than previously indicated, and that the major event at the Miocene/Pliocene boundary was in fact mostly an ecological turnover and restructuring of the benthic faunas. This was associated with a change in climate and immigration of cooler water taxa from areas outside of New Zealand when the circum-Antarctic current intensified (Beu, 1990; Beu et al., 1997). Fleming (1965) described this fauna as the "neoaustral faunal element". This Late Miocene cooling event was much more rapid than the gradual cooling that had been occurring since the mid-Miocene's Lillburnian stage (see Hendy, 2009; figure 2D).

Possible causes for this pattern of calculated FADs

Immigration

FADs may frequently imply immigration into a region rather than speciation within it (Schankler, 1981)and Beu and Maxwell, (1990), have suggested that the high number of FADs in the Middle Eocene is due to abundant immigration of mollusks into New Zealand. The peak of implied first appearances of *Zeacolpus* suggested by the phylogeny (see figure 3.4) may, therefore, be a reflection of this genus' immigration into New Zealand at this time. It would be, however, unusual for 10 species of the same genus to have immigrated independently at the same time, suggesting that while

an ancestor of the genus may have arrived in New Zealand as part of this pulse of immigration, speciation then likely occurred *in situ*.

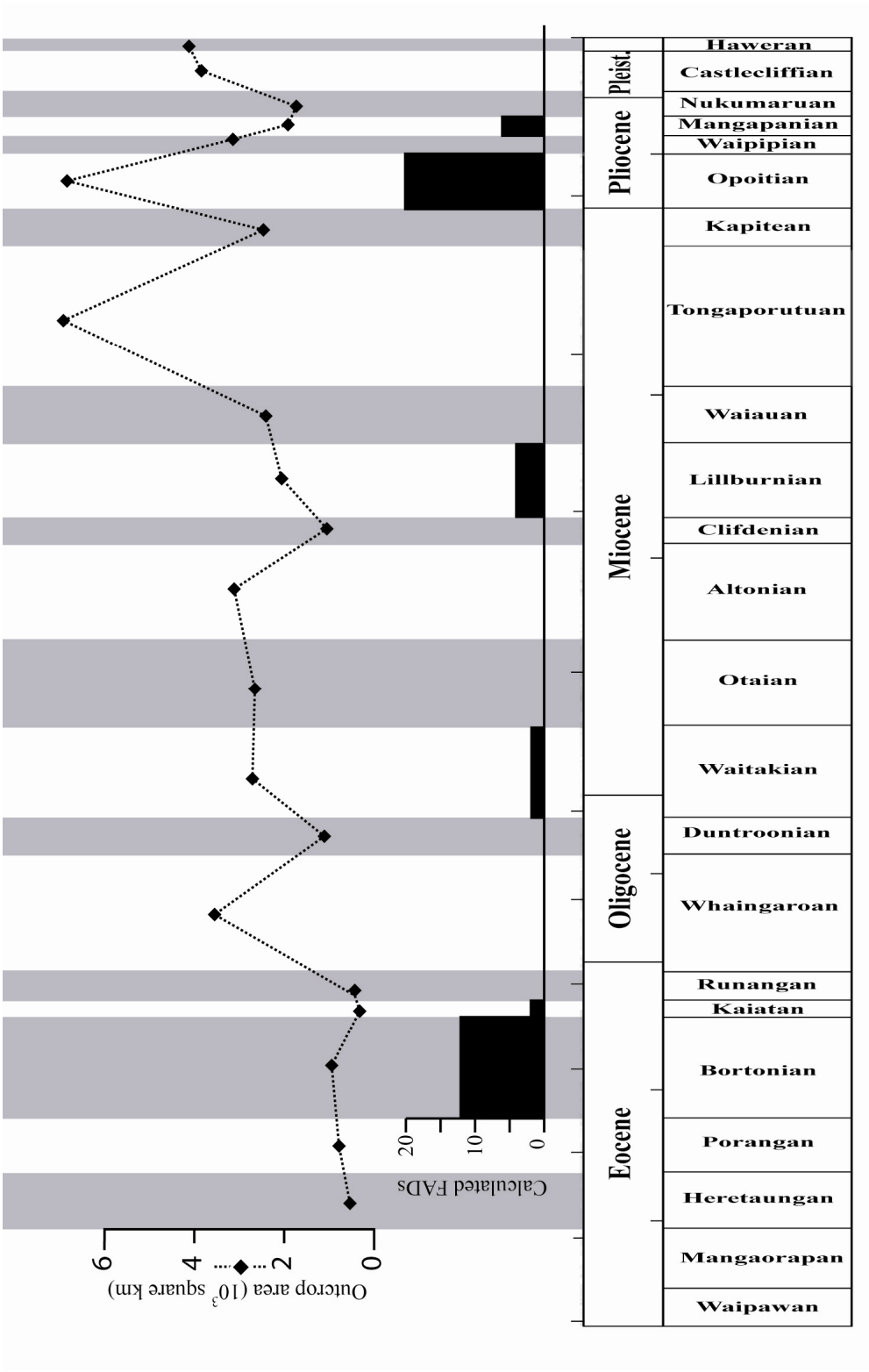
The first appearance of the genus *Stiracolpus* corresponds to the appearance of the previously discussed cool-water fauna that began to appear at the end of the Miocene, and it may therefore be that immigration is entirely responsible for the peak in FADs at this time. However, it is again unlikely that such a large number of species immigrated separately all at once without leaving any trace of any ancestors elsewhere, making it more probable that an ancestor immigrated into New Zealand and then speciated *in situ*.

Artifact

Peaks in FADs and diversity may be artifacts due to high sampling intensity relative to other time periods, causing an inflated number of species to be seen. This is likely not the case here, as the stages in which large numbers of raw FADs are seen (e.g., the Bortonian) are periods of both low diversity and low rock volume (Beu, 1990; Crampton et al., 2003) and relatively low sampling intensity (Hendy, 2007) (figure 3.6).

While these peaks are probably not within-stage sampling artifacts, it is possible that they may be artifacts due to poor sampling prior to the stage in which the peak occurs. If a species originates in one earlier stage but is not sampled in that stage due, for example, to low rock volume, its FAD will be recorded later. If a stage is systematically under-sampled for any reason, the result will be an artificially inflated peak in a later stage where the rock record is better. The cluster of implied *Zeacolpus*

Figure 3.6: Outcrop area adapted from Crampton et al. 2003 shown against calculated originations based on phylogenetic relationships of the two genera *Stiracolpus* and *Zeacolpus*. In the case of both the Bortonian and Opoitian peaks of originations the stages prior both relatively low outcrop area. The Bortonian peak in origination occurs in a stage that also has low outcrop area suggesting that this peak is not an artifact of poor sampling within the stage, but possibly of poor sampling in previous stages artificially inflating the FADs seen in the Bortonian.


Haweran
Pleist.
Castlecliffian
Nukumaruan
Mangapanian
Pliocene
Waipipian
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Miocene
Altonian
Otaian
Waitakian
Duntroonian
Oligocene
Whaingaroan
Runangan
Kaiatan
Bortonian
Porangan
Heretaungan
Mangaorapan
Eocene
Waipawan
Calculated FADs
0
10
20
Outcrop area (10³ square km)
0
2
4
6

FADs in the Bortonian (figure 3.2) may be such an artifact of sampling caused by the Bortonian being the first stage in which *Zeacolpus* is found: speciation may have occurred at some point prior to this stage but not be seen due to poor preservation or low availability of strata. The outcrop area of New Zealand Paleocene to Early Eocene and the collection intensity of these rocks is extremely low (see Crampton et al., 2003; figure 2) and the faunas are therefore poorly known relative to other periods of the New Zealand Cenozoic. This explains part of the temporal distribution of turritellids in the Early Cenozoic: there is a considerable period between the earliest known turritellid in the New Zealand fossil record (*Leptocolpus semiconcavus* in the Teurian stage of the Paleocene, see figure 3.1) and the next known turritellid occurrences (*Zeacolpus gagei*, *Spirocolpus waihaoensis* and *Amplicolpus wellmani* in the Bortonian). Therefore, speciation may have occurred, either from an ancestor already present in the earlier stages of the Eocene and Paleocene or from one that immigrated prior to both the observed and implied peak of first occurrences in the Bortonian.

A similar situation may also account for the pattern observed in *Stiracolpus* in the Pliocene (figures 3.2 and 3.3). The ancestor of *Stiracolpus* may have appeared in New Zealand during the Late Miocene or very Early Pliocene and then radiated. As with the first appearance of *Zeacolpus* it is difficult to constrain the timing of the appearance of the first *Stiracolpus*. The rocks at the end of the Miocene contain a depauperate mollusk fauna partially due to the strata largely representing bathyl rather than shelf environments. There are large sediment volumes of this age and collection intensity has been high so this appears to be a real signal rather than a sampling artifact (e.g., see Crampton et al., 2003).

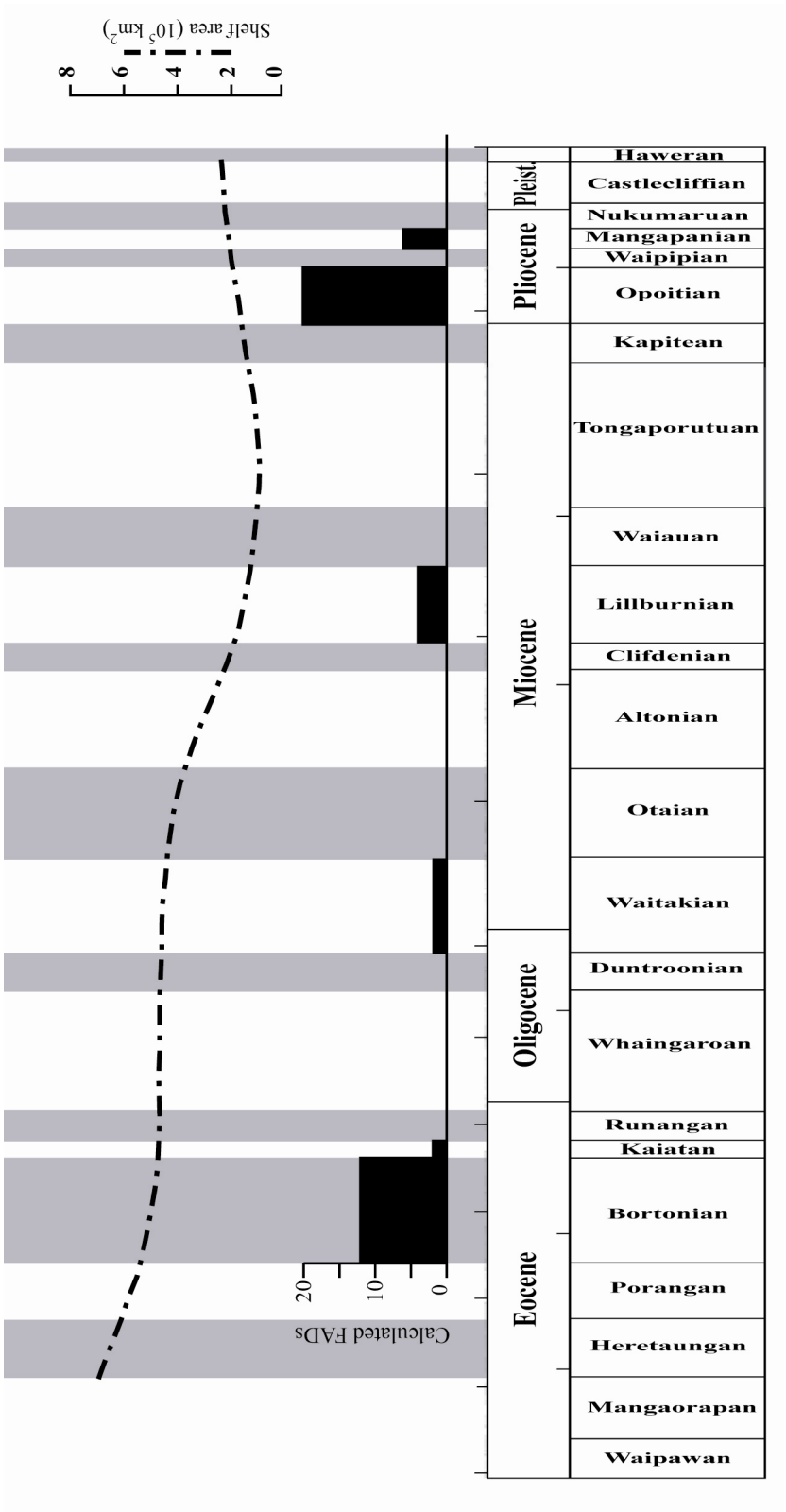
Sea level change

There is not currently an adequate sea level curve for the Cenozoic of New Zealand due to the extreme difficulty in untangling the impacts of global sea level variation from the various local tectonic effects on sea level. Previously (e.g., see Crampton et al., 2006b), estimated shelf area has been used as a proxy for sea-level in the older stages of the Cenozoic, but this curve lacks detail as it is drawn from relatively few data points (figure 3.7). This makes it difficult to examine the impact of sea level change on evolutionary patterns. However, there are some potential correlations of sea level change with origination data.

In 1956, Wilson described a transgression from the Late Cretaceous to a maximum highstand during the Oligocene Waitakian stage (see also Crampton et al., 2003). This highstand coincides with a small peak in calculated *Zeacolpus* originations that is seen in the Waitakian. Some studies cite periods of maximum speciation occurring during periods of highstand, attributing speciation concurrent with local transgressions to increases in available habitat area (e.g., Kauffman, 1973; Dockery, 1986; Geary, 1990; McKinney and Allmon, 1995). It has been suggested that an increase in habitat area may lead to species expanding into new areas and differentiating (e.g., Hansen, 1988), and increased persistence of these populations could lead to new species if the environment remained stable, such as during an extended high-stand period (McKinney and Allmon, 1995).

Since Wilson's (1956) paper a series of regressions and hiatuses has been identified through the Paleogene part of the New Zealand sequence, including one at the base of

Figure 3.7: Shelf area curve adapted from Crampton et al., 2006 shown against calculated originations based on phylogenetic relationships of the two genera *Stiracolpus* and *Zeacolpus*. This shelf area curve has been used as a proxy for sea level change but is based on few data points. There is not currently a sea level curve for the New Zealand Cenozoic due to the difficulty of calculating one in such a tectonically active area.


Shelf area (10^5 km^2)
8
6
4
2
0
Calculated FADs
20
10
0
Pleist.
Pliocene
Miocene
Oligocene
Eocene
Haweran
Castlecliffian
Nukumaruan
Mangapanian
Waipipian
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Altonian
Otaian
Waitakian
Duntroonian
Whaingaroan
Runangan
Kaiatan
Bortonian
Porangan
Heretaungan
Mangaorapan
Waipawan

the Bortonian (see Beu and Maxwell, 1990) that appears to occur across a wide geographic range and probably lasted a few hundred thousand years before transgression resumed. Regression can lead to allopatric speciation via habitat fragmentation, a mechanism that has previously been proposed for speciation in Gulf Coast turritellids in which high origination rates are seen during regressions (McKinney and Allmon, 1995).

While changes in sea level may cause or contribute to speciation, there are a number of preservation biases caused by the sea level change itself which can obscure the pattern (e.g., Jablonksi, 1980, Holland, 2000). In the pre-Pliocene strata of New Zealand, the detailed stratigraphic control required to disentangle possible biases introduced by sea level change is lacking. Additionally, as discussed above, the actual originations may be stratigraphically older than the stages in which they are counted, and may not correlate with these sea level fluctuations. A higher level of temporal resolution of strata and speciation events than is available for the pre-Pliocene of New Zealand would be necessary to fully elucidate causes of speciation.

Temperature

The late Early Miocene and early Middle Miocene (Altonian-Clifdenian) was the warmest period of the New Zealand Cenozoic (figure 3.8 and Beu, 1990) after the Paleocene-Eocene Thermal Maximum. An apparent influx of warmer-water molluscan taxa has been observed in the Otaian and Altonian stages (Beu and Maxwell, 1990), though this is not seen in the FADs calculated here for *Zeacolpus* and *Stiracolpus*. After this Miocene thermal maximum, a drop in temperature inferred in

Figure 3.8: Paleotemperature curves. Local marine paleotemperature (originally adapted from Hornibrook, 1992) and $\delta^{18}O‰$ curves (originally adapted from Zachos et al., 2001) shown against calculated originations based on phylogenetic relationships of the two genera *Stiracolpus* and *Zeacolpus*.

δ18O(‰)
0
1
2
3
4
Haweran
Castlecliffian
Pleist.
Nukumaruan
Mangapanian
Waipipian
Pliocene
Opoitian
Kapitean
Tongaporutuan
Waiauan
Lillburnian
Clifdenian
Miocene
Altonian
Otaian
Waitakian
Duntroonian
Oligocene
Whaingaroan
Runangan
Kaiatan
Bortonian
Porangan
Heretaungan
Mangaorapan
Waipawan
Eocene
Calculated FADs
20
10
0
Shallow water
marine climate (°C)
25
20
15
10

the Lillburnian (figure 3.8), which marks the beginning of a gradual cooling event that continued to the end of the Miocene when abrupt cooling was associated with increased circulation of cold water in the circum-Antarctic currents. There is also a terminal Miocene turnover in the molluscan faunas of Chile at this time caused by the same northward movement of the Humboldt Current (Beu and Maxwell, 1990).

Two genera of turritellids, *Tropicolpus* and *Amplicolpus*, disappeared at the end of the Middle Miocene thermal maximum. Neither of these is present in the rock record past the end of the Clifdenian when the Late Miocene cooling began (see Beu and Maxwell, 1990). Nine *Zeacolpus* species (50% of those in the analysis) had also become extinct by this time (figure 3.4), with another four disappearing within a further three stratigraphic stages as temperatures cooled. All other species except three become extinct by the end of the Miocene.

There is a peak of origination of *Zeacolpus* species in the Lillburnian, coinciding with the onset of cooling (figure 3.8). One of the species implied to have originated at this point is *Zeacolpus vittatus*, which is the only representative of the genus to survive through the cooler Pliocene and into the Recent. While *Z. vittatus* persists into the Recent, the other two *Zeacolpus* species, and most species of *Maoricolpus* that persisted past the end of the Miocene, disappear during previously noted extinctions at the end of the Pliocene stages (e.g., see Beu, 1990; Beu and Maxwell, 1990). These extinctions appear to occur rapidly at the end of stages but this is in part an artifact of species range data being counted as filling an entire stage; and the actual extinction events are likely to have been more gradual (Beu and Maxwell, 1990).

Conversely, as species of *Zeacolpus* and other genera that persisted past the Miocene thermal maximum were becoming extinct, *Stiracolpus* appears to have undergone a radiation, with multiple new species arising in the first stage of the Pliocene (Opoitian) and in the later Pliocene (Mangapanian). These peaks of calculated origination occur during periods in which origination rates for the entire molluscan fauna are very low (figure 3.9 and Crampton et al., 2006a), as is also the case for the Lilliburnian peak in *Zeacolpus* origination (figure 3.5). With the exception of this origination peak associated with cooling in the Lillburnian, *Zeacolpus* as a whole appears to have been less tolerant of cool conditions than *Stiracolpus*, with all but one species becoming gradually extinct through the cooling Miocene to Pleistocene. Today, the geographic distribution of the one *Zeacolpus* species to have survived, *Z. vittatus* (which appears to have originated during a period of cooling) is the same as *M. roseus*. Both species' distributions are very similar to the modern geographic distribution of *Stiracolpus* species, implying similar temperature tolerances.

Turritellid gastropods worldwide show a documented trend through time of a change in habitat preference from warm to cooler conditions (Allmon, 2007), as well as from carbonate environments to siliciclastic environments from the Cretaceous to the Neogene. The pattern seen here fits with this observation; a warmer-water genus (*Zeacolpus*) becomes gradually extinct as temperatures cool leaving a single survivor that is tolerant to cooler conditions, while another genus better able to survive in cool waters radiates instead. Additionally, two other genera of turritellids in the New Zealand Cenozoic, *Tropicolpus* and *Amplicolpus* also become extinct when temperatures begin to cool after the Miocene thermal maximum (see range charts in Beu and Maxwell, 1990), suggesting that these genera were also warm-water taxa that did not survive the change to cooler conditions.

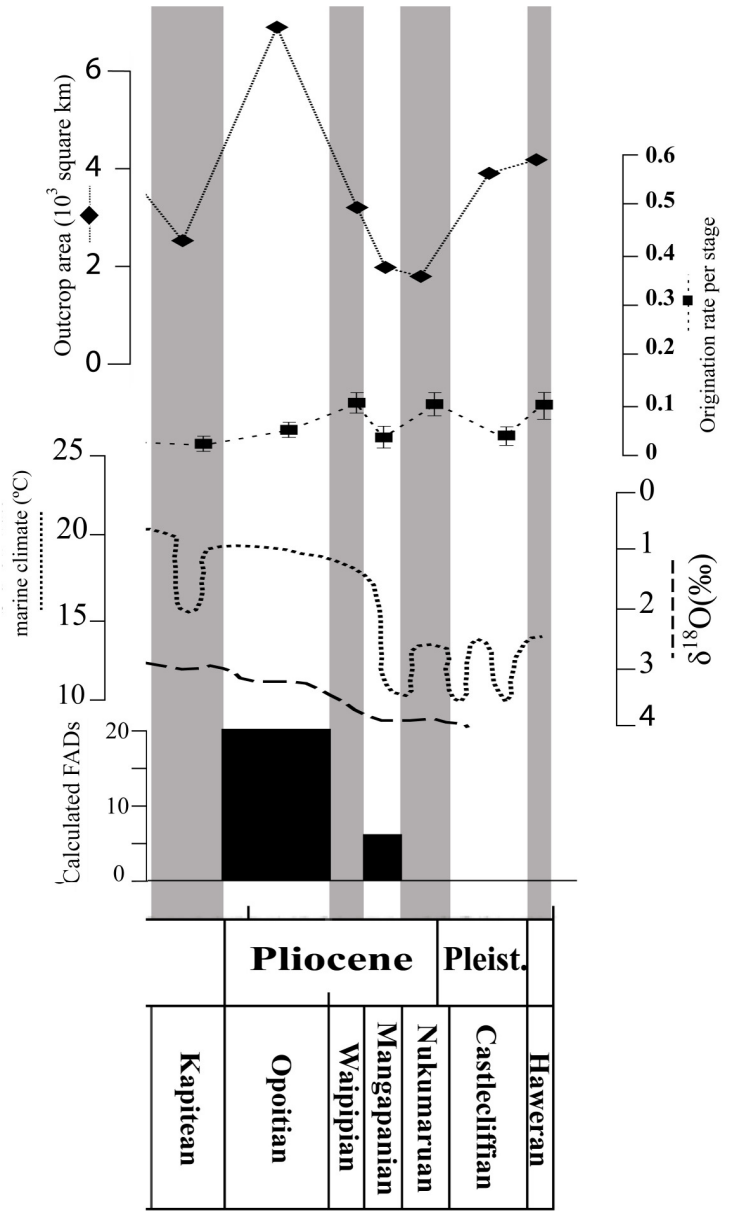


Figure 3.9: Paleotemperature curves diversity curves and outcrop area curves (see legend for figure 3.5) for the Pliocene and Pleistocene shown with calculated origination peaks (bottom bar chart). Both peaks occur during periods where temperature decreases, though the Mangapanian temperature drop is of greater magnitude and occurs over a shorter interval. The Opoitian temperature decrease is gentle but the Hornibrook, 1992, curve does indicate a short term temperature excursion in the last stage of the Miocene immediately before the Opoitian origination peak. The Opoitian peak occurs during a peak of high origination for the entire molluscan fauna thought to be linked to a period of high immigration rates (Beu and Maxwell, 1990) whereas the Mangapanian peak for *Stiracolpus* occurs while background origination rates are low.

The implied FAD peak during the Opoitian is associated with the change from a warmer Miocene fauna to a cooler Pliocene fauna when the end-Miocene cooling event occurred, when the ancestor of *Stiracolpus* is inferred to have immigrated into New Zealand. However, the radiation that then occurred would have been influenced by local conditions. While the Opoitian was the warmest part of the Pliocene, with temperatures dropping through the stage into the Waipipian and then dramatically into the Mangapanian (figure 3.9), there is a significant cooling event in the preceding Kapitean stage. As noted above, it is also possible that the peak in the Opoitian is partially an artifact of origination occurring earlier but not being sampled, and if this is the case, it is possible that this peak in originations is linked to this episode of cooling in the Kapitean.

Similarly, the peak of originations in the Eocene Bortonian stage occurred during a period that was warm relative to the preceding and following stages (figure 3.8). While it is possible that these relatively warmer conditions are linked in some way to the origination peaks, there is also a cooling event in the Porangan stage immediately prior to the Bortonian which may be responsible. However, the small peak in the Kaiatan stage following the Bortonian occurs after at least 6My of warmth which is less likely to be linked to an earlier cooling phase. As argued above, *Zeacolpus* species generally appear to prefer warmer conditions than *Stiracolpus* species and it is therefore possible that this Eocene radiation of *Zeacolpus* was not caused by the same mechanisms as the other radiations discussed here.

Cooling events may also coincide with the smaller FAD peak in the later Pliocene Mangapanian stage (figure 3.9). Several lines of evidence suggest multiple pulses of

cooling in the New Zealand Pliocene, including the distribution of cool-water macrofauna (e.g., Fleming, 1944; 1953; Beu and Maxwell, 1990; Beu et al., 1997), cool-water microfossils (e.g., Jenkins, 1968), pollen (e.g., Mildenhall and Harris, 1970), terrestrial and marine glaciogenic strata (e.g., Gage, 1961; discussion by various authors in Suggate et al., 1978), and oxygen isotopes (e.g., Devereux et al., 1970; Zachos et al., 2001; Nelson and Cooke, 2001). These have all been dated biostratigraphically, and so the temporal resolution of when cooling periods occurred in New Zealand has been relatively poor. Compiled temperature curves (e.g., Hornibrook, 1992) have been only semi-quantitative (Crampton et al., 2006b).

A more recent temperature reconstruction (Carter, 2005) has used gamma radiation logs from ODP site 1119 off the east coast of the South Island as a proxy for ice volume and therefore temperature. Gamma radiation signals vary distinctly between terrigenous muds and silts deposited during glacial periods and calcareous sands of interglacial periods because of the variation in potassium content between these two rock types. This record has a 1-2 k.y. resolution in the mid-Pliocene. Carter (2005) suggests Pliocene cooling occurred around the Mangapanian/Nukumaruan boundary (c2.4Ma), the Waipipian/Mangapanian boundary (c3.0Ma), and in the Waipipian (c3.5Ma). Two of these cooling pulses (the base Mangapanian and possibly the earlier Waipipian event) could be implicated in the implied FAD peak seen here. While the Waipipian cooling suggested by Carter is supported by planktonic foraminifera isotope data (Vella et al., 1975), it is contradicted by interpretation of the molluscan fauna of the stage (Fleming, 1953; Beu, 1974) that does not indicate that cooling occurred. Possible explanations for this contradictory evidence have included stratification of the water column or time averaging over the course of a cyclothem sequence mixing the mollusks and foraminifera but the detailed sequence stratigraphy

necessary to clarify this has not been carried out (Carter, 2005). It is also possible that any cooling that occurred at this point did not affect the bottom waters in which the molluscan fauna was living, only the surface waters.

The impact of temperature variation on standing diversity is well studied (e.g., see Evans et al., 2005 for a review), with warmer temperatures being linked to higher diversities (e.g., Evans et al., 2005; Clarke and Gaston, 2006; Mayhew et al., 2008; see also Erwin, 2009) However, most of this literature examines diversity rather than speciation, normally citing reduced extinction rates as the driver of high diversities rather than increased speciation. In fact, temperature drops have more usually been linked with extinction events rather than radiations (e.g., Hansen, 1987; 1988). It is therefore possible that despite the correlations seen here, cooling events may not be causing speciation and that other environmental factors correlated with temperature change which cannot be seen in the available dataset are more important. For instance, decreasing temperatures during the Pliocene and Pleistocene are linked with the occurrence of glaciation which reduces sea level, making possible drivers of radiation difficult to disentangle. For instance, local sea level can lead to speciation (through the formation of peripheral isolates leading to speciation in allopatry; McKinney and Allmon, 1995) but range limitation may also be caused by decreasing temperatures in a similar way (e.g., see Evans et al., 2005).

While peaks of calculated origination of *Stiracolpus* occur in two stages of the Pliocene, there are none in the later Castlecliffian of the Pleistocene despite glacial cycles occurring during this stage also. This suggests that the causal mechanisms may have changed through time, or that they are controlled by a variety of factors besides temperature. For instance, oxygen isotope curves (figure 3.9 and Carter, 2005)

indicate the Castlecliffian was cooler overall than the Opoitian and Mangapanian, perhaps putting it below some temperature threshold at which species will be unable to respond to changing environmental factors by speciating. While the environmental data necessary to elucidate these questions may never be available in pre-Pliocene sediments, it may be possible in the future to do so in the Pliocene and Pleistocene. Detailed correlation of formation level origination data with the sequence stratigraphy and oxygen isotope stages may help to clarify why speciation does not appear to be occurring in *Stiracolpus* after the end of the Pliocene.

Whatever the underlying mechanisms that triggered speciation in these genera, it is clear that *Zeacolpus* and *Stiracolpus* have responded differently to environmental change in the Pliocene, with *Stiracolpus* undergoing a radiation while *Zeacolpus* became largely extinct. Why *Stiracolpus* and *Zeacolpus* reacted so differently is not currently clear. It is possible that the difference in size between the two genera may be important, as there is some evidence suggesting that larger turritellids may be better adapted to warmer conditions than to cooler conditions. For instance the largest turritellids in the New Zealand Cenozoic (*Amplicolpus cavershamensis*), occurred during the warmest part of the Miocene and the majority of the biggest turritellid species become extinct when temperatures become cooler (see range data in Beu and Maxwell, 1990). However, both *Z. vittatus* and *M. roseus*, while not as tall or wide as species of *Amplicolpus* do grow to lengths much greater than those of *Stiracolpus* and are not unusual in size for their genera.

A previous study (Teusch and Guralnick, 2003) found that smaller turritellids occurred in cooler conditions in the Miocene-Recent of the Gulf of Chile due to reduced growth rates. However, there was also a change in productivity over this period and a

productivity influence on size may be conflated with the influence of temperature. *Stiracolpus* species have similar numbers of whorls to *Zeacolpus*, so it is possible that their relatively smaller size is also caused by a reduced growth rate, making them better able to survive in cooler climates. To ascertain if this is the case, growth rates from stable isotope measurements of species of both genera would be required.

Conclusions

These results suggest that peaks in origination of New Zealand turritellid species throughout the Cenozoic (raw or implied) are not linked to a single causal mechanism. Rather, they appear to be due to a combination of 1) preservation bias in preceding stages, 2) immigration from other biogeographic areas, and 3) abiotic factors such as temperature and sea level change. Of these, temperature appears to have the clearest link with origination rates here, with cooling temperatures apparently correlated with periods of high origination as well as peaks in extinction.

When ghost ranges implied by phylogeny are taken into account, the distribution of first appearances for *Zeacolpus* and *Stiracolpus* appear very different from raw FADs. For both genera, it is difficult to further constrain the upper range of timings of first occurrences given the depauperate nature of the facies of the stages immediately preceding them.

The ancestor of *Zeacolpus* may have arrived during the Bortonian or in the stages beforehand which are poorly sampled, and appears to have subsequently speciated *in situ*. The earliest time this may have occurred is hard to pin down, but may have been as early as the first stage of the Paleocene, the Teurian (65-55.5Mya), though it is

more likely to have occurred in the stages immediately prior to the Bortonian (e.g., the Porangan, 46.2-43Mya). This implies a range of time in which speciation may have occurred 65-37Mya, though it likely occurred towards the later end of this period, 46.2-37Mya. Similarly, *Stiracolpus* appears to have undergone an endemic radiation after an ancestor immigrated to New Zealand in the Late Miocene or Early Pliocene. The earliest data ate which this may have occurred is hard to infer, but it must have been no later than the end of the Opoitian at 3.6Mya.

Crampton et al. (2006b) could not demonstrate a link between paleotemperature and biodiversity in the New Zealand molluscan record, as available temperature curves were inadequate to the task. For the same reason, it is not possible to conclusively demonstrate a link between peaks in origination and paleotemperatures here, as the Zachos et al., (2001) and Hornibrook (1992) data are still the only available paleotemperature curves. However, despite the problems associated with both of these paleotemperature curves there does still appear to be a correlation between times of cooling temperature and peaks of origination, suggesting a link between decreasing temperature and speciation. This is possibly due to the initiation of allopatric speciation by range reduction.

While temperature may be the factor most obviously correlated with peaks in origination rate here, other environmental factors (such as variation in sea level) may also have contributed to the pattern. This is hard to ascertain given the poor sea level record in the pre-Neogene strata. Even in the Pliocene and Pleistocene, where the record is better, fluctuating temperatures in the area are linked with changes in sea level caused by glaciation and the two signals are hard to separate. Though sea level change may be contributing to the observed pattern, it is thus probably not the sole

driver of speciation. Though a sea level change is associated with most of the implied FAD peaks seen here, origination is not consistently tied to transgressions or regressions: it is linked to transgression in the Bortonian, a highstand in the Waitakian and sea level decreases in the Pliocene. More detailed first appearance dates for the higher resolution Pliocene and Pleistocene sequences would be required to further test this correlation and possible causation. Given the quality of the rock record and level of stratigraphic control in the Pliocene of New Zealand, this should prove a fruitful avenue for future research.

The current lack of adequate paleotemperature data and well constrained sea-level curves for most of the pre-Pliocene in New Zealand is problematic and prevents causes of speciation events in *Zeacolpus* from being confidently inferred, especially if, as is possible, the group's response to environmental variation changed through time. However, there is potential in the Pliocene and Pleistocene for more detailed work to be carried out linking speciation events with environmental change. Well-constrained local sea level curves for much of the Pliocene and Pleistocene based on detailed sequence stratigraphic work are being produced (e.g., see Naish et al., 1998; Naish, 2005; Naish et al., 2005b; Naish et al., 2005a) allowing potential correlation of originations to precise cyclothem sequences, but this will not eliminate the difficulty of separating linked variations in sea level and temperature.

In this case, to further constrain the causes of speciation in *Stiracolpus*, it would be necessary to correlate the origination of species to specific oxygen isotope stages, as Beu (2004) has done with bivalve species lists by correlating taxa from Fleming's 1953 formations with the oxygen stages of Naish et al., (1998) and Carter and Naish, . Most *Stiracolpus* species were described after 1953, making it harder to correlate their

occurrence data with oxygen isotope stages. However, it should be possible to correlate stratigraphic data from Marwick's original descriptions to oxygen isotopes even though these did not always utilize Fleming's formations. More modern datasets that include turritellid specimens collected within the modern sequence stratigraphic nomenclature (e.g., see Hendy, 2007; Hendy and Kamp, 2007) are currently only available to generic level. To correlate species appearances with isotope stages will therefore require further collection and identification of specimens to species level.

Stiracolpus is more tolerant of the cooler temperatures of the post-Miocene than *Zeacolpus* which did not radiate during the Pliocene, (though see discussion above with regard to the Lillburnian radiation of *Zeacolpus*). *Stiracolpus* appears to be unusual amongst the New Zealand turritellid genera in being tolerant of cooler conditions. Amongst other genera there are individual species that have survived in cooler environments, but most, such as *Amplicolpus*, *Tropicolpus*, and the majority of *Zeacolpus* species disappear when temperatures decrease. The exception to this is *Z. vittatus* which appears to have originated with the onset of cooler temperatures in the Middle Miocene Lillburnian stage and survived through the Pliocene into the Recent. This pattern shows a gradual replacement of warm-water species by cool-water species from other genera as the warm-water species became extinct. This agrees with Allmon's (2007) observation that turritellid gastropods today do not have the same environmental tolerances as stratigraphically older members of the family, being found in cooler waters than in the past. Until *Zeacolpus* and *Stiracolpus* can be placed into a larger phylogenetic framework, it is not possible to differentiate between Allmon's three potential causes of environmental shift.

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APPENDIX 1

Conus species plates.

Figure A1: Scale bar is 1cm in each case.

a) *Conus abbreviatus* PRI 1150F
b) *C. anemone* CAS 179333
c) *C. araneosus* CAS 180435
d) *C. archon* CAS 180106
e) *C. arcuatus* CAS 178030
f) *C. balteatus* CAS 180439
g) *C. bandanus* CAS 179330
h) *C. brunneus* CAS 178041
i) *C. californicus* PRI 683F
j) *C. catus* PRI 1145F
k) *C. chaldaeus* PRI 3708H
l) *C. cinereus* CAS 180460

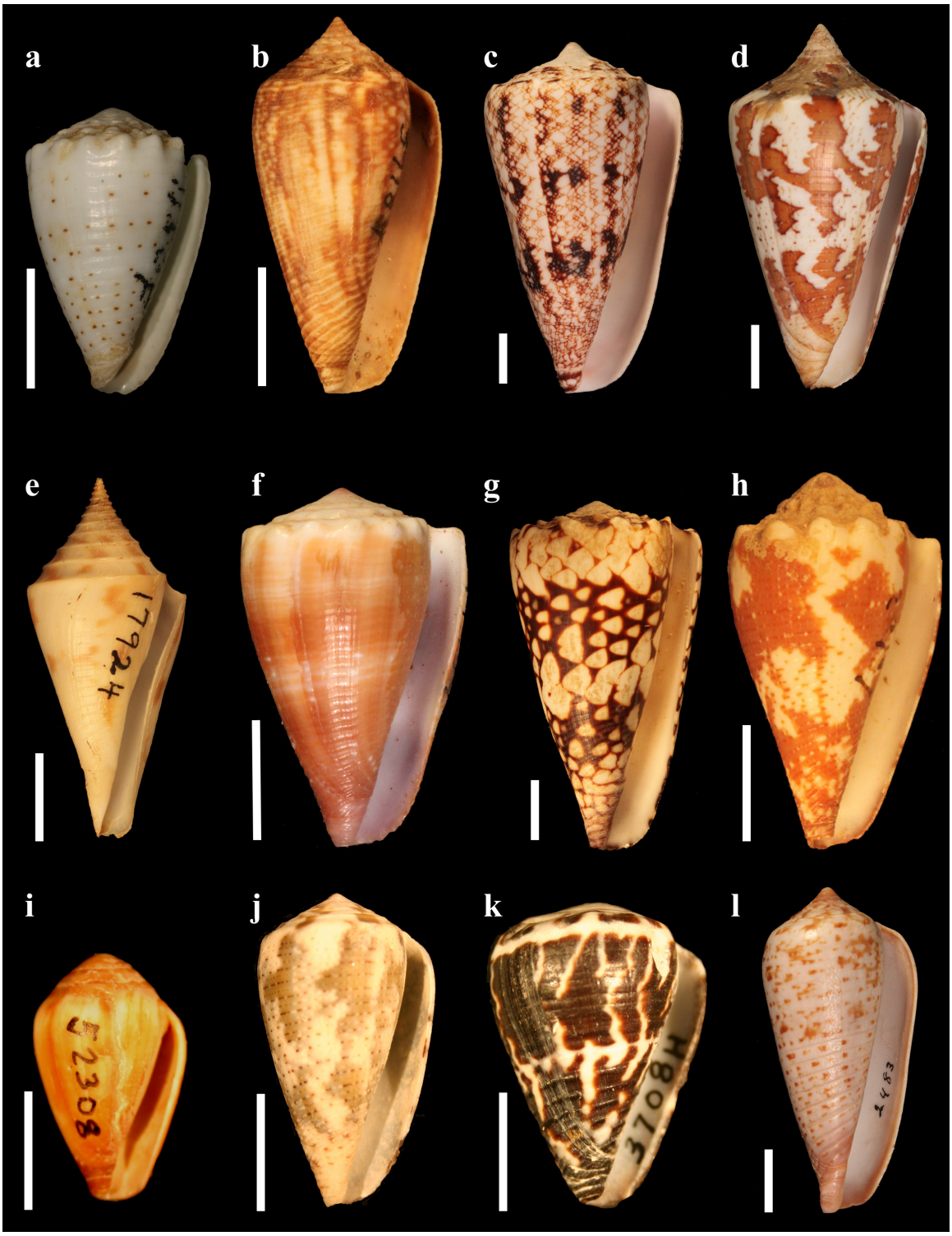
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Figure A2: Scale bar is 1cm in each case.

a) *Conus coronatus* PRI 2370C
b) *C. dalli* CAS 179339
c) *C. daucus* PRI 46089
d) *C. diadema* CAS 180449
e) *C. distans* CAS 179304
f) *C. dorreensis* CAS 178043
g) *C. ebraeus* PRI
h) *C. eburneus* PRI 11764
i) *C. episcopatus* CAS 180455
j) *C. figulinus* PRI
k) *C. flavidus* PRI Acc1404
l) *C. furvus* CAS 179346

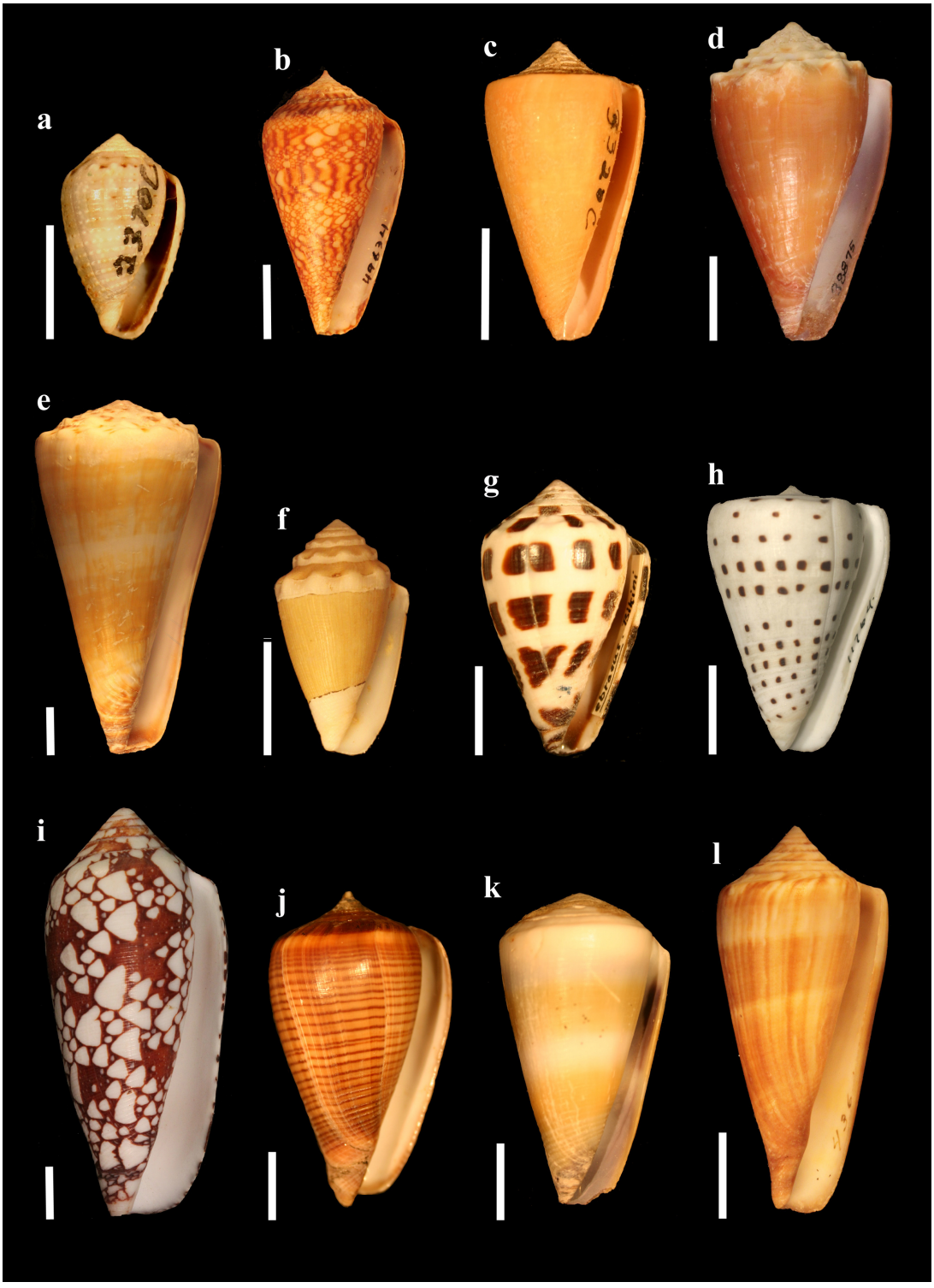
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Figure A3: Scale bar is 1cm in each case.

a) *Conus generalis* PRI Acc 791
b) *C. geographus* CAS 179320
c) *C. gladiator* PRI 1573F
d) *C. imperialis* PRI Acc 1084
e) *C. jaspideus* PRI 4298C
f) *C. leopardus* PRI
g) *C. lithoglyphus* PRI
h) *C. lividus* PRI 38515
i) *C. magus* PRI 11833
j) *C. mahogani* PRI 4903E
k) *C. marmoreus* PRI 11757
l) *C. miles* PRI

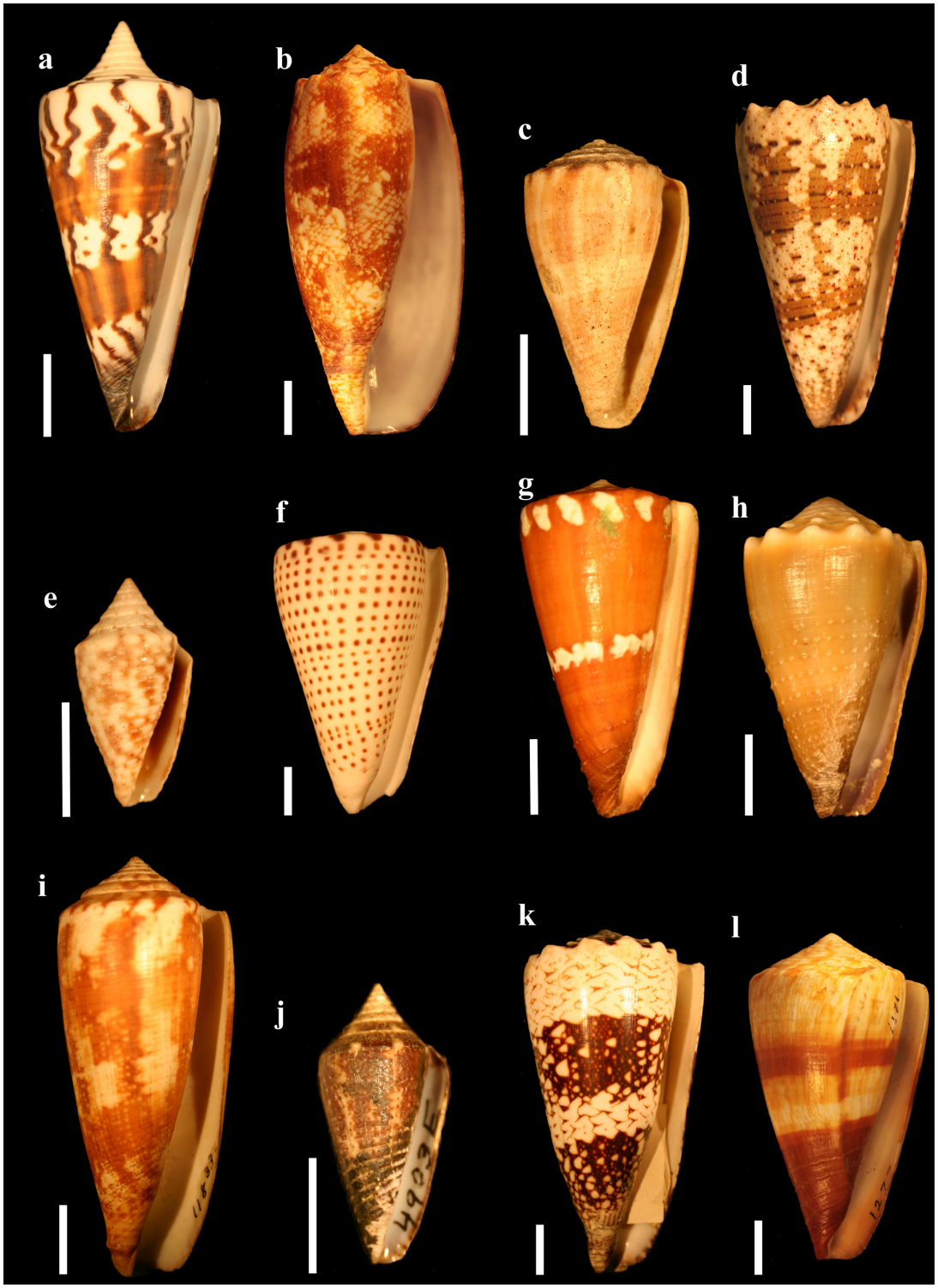
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Figure A4: Scale bar is 1cm in each case.

a) *Conus miliaris* PRI Acc791
b) *C. mus* PRI 4444F
c) *C. musicus* CAS 179321
d) *C. nux* PRI Acc 1267
e) *C. omaria* PRI
f) *C. patricius* CAS 179311
g) *C. pennaceous* CAS 179308
h) *C. perplexus* PRI 2680H
i) *C. planorbis* PRI 2373C
j) *C. princeps* PRI 506E
k) *C. pulicarius* PRI Acc 2056
l) *C. purpurascens* PRI Acc 1267

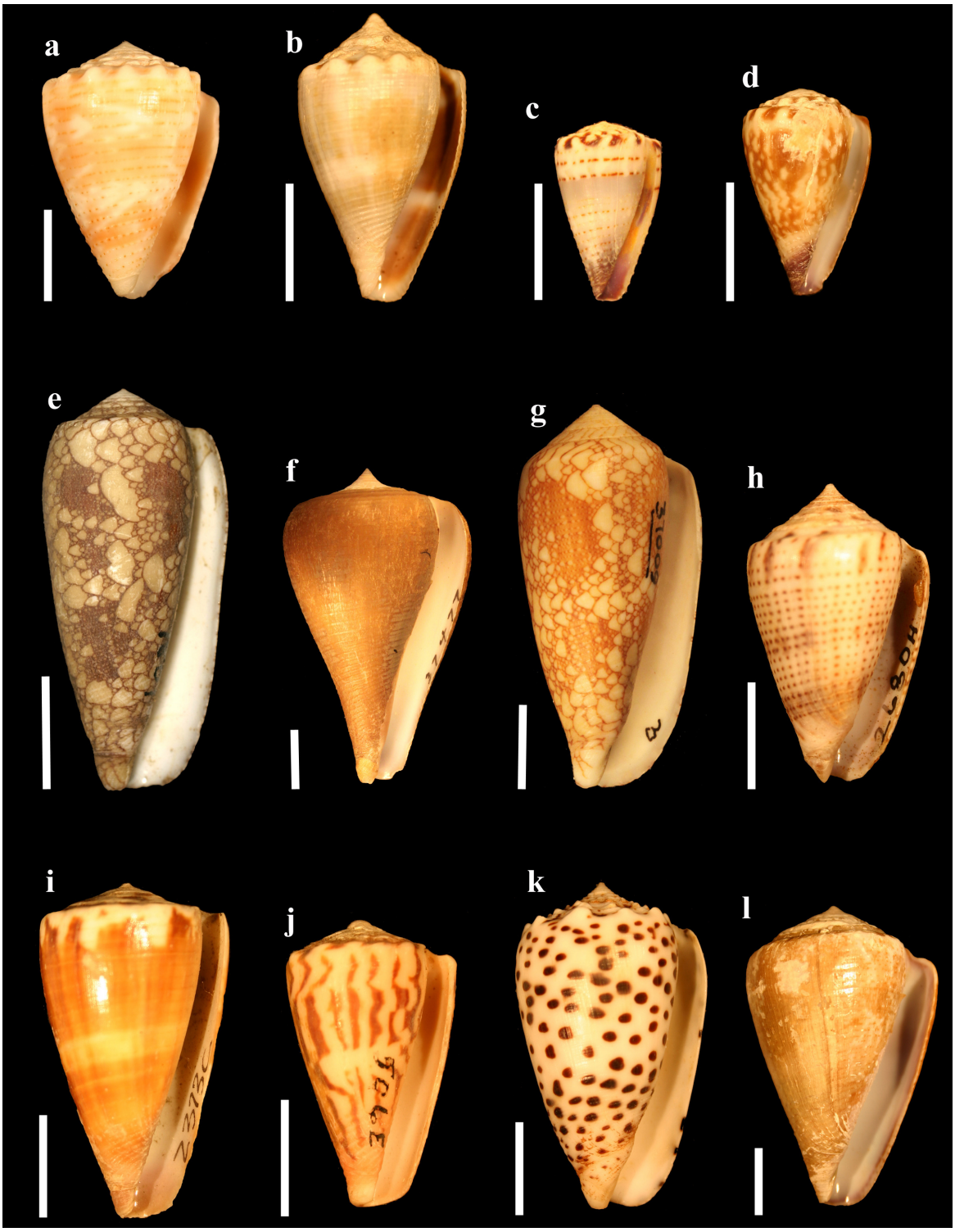
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Figure A5: Scale bar is 1cm in each case.

a) *Conus quercinus* PRI 54497
b) *C. rattus* CAS 178083
c) *C. regius* CAS178046
d) *C. sponsalis* PRI 3655H
e) *C. stercusmuscarum* CAS 179316
f) *C. striatus* PRI 4708H

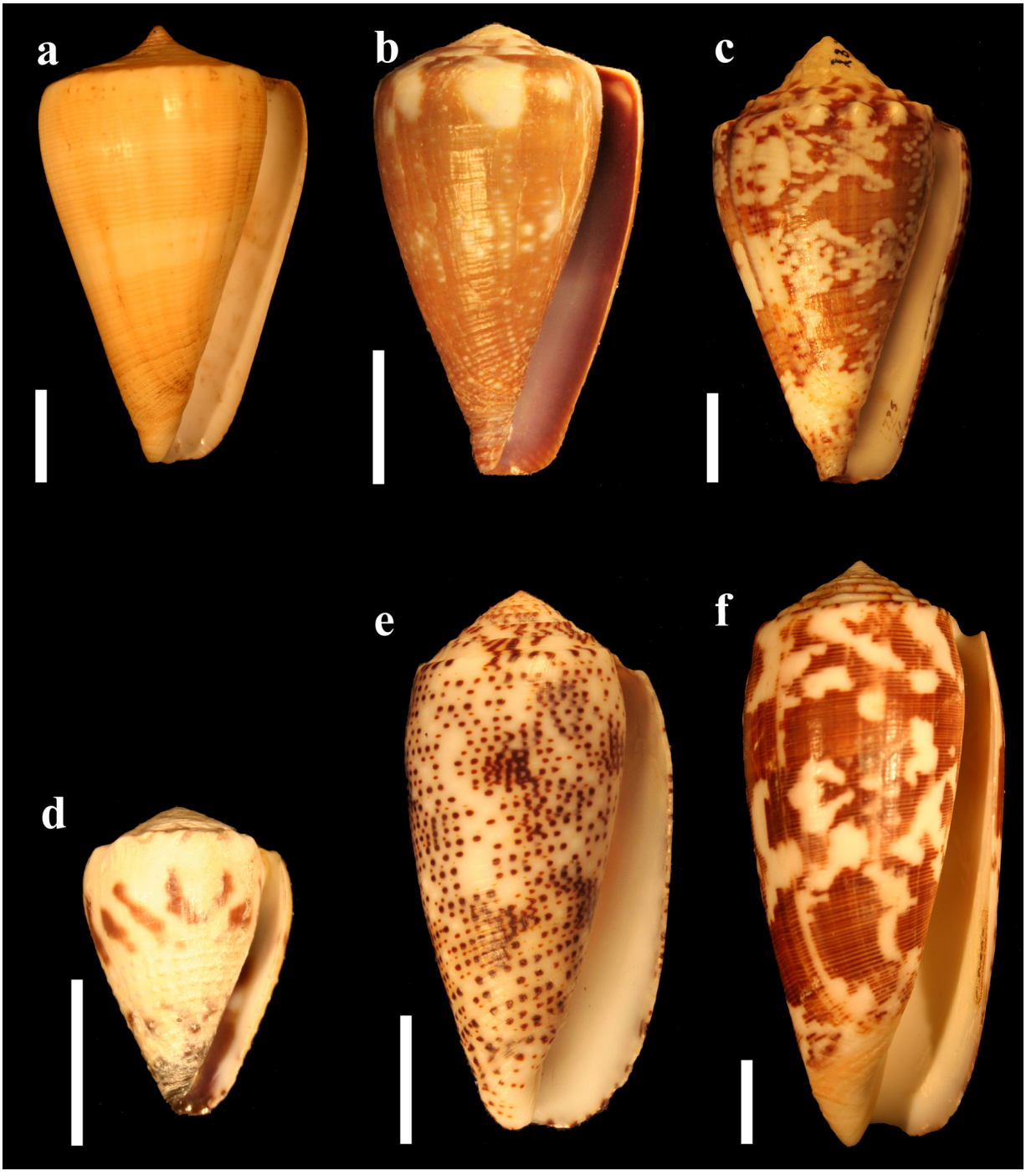
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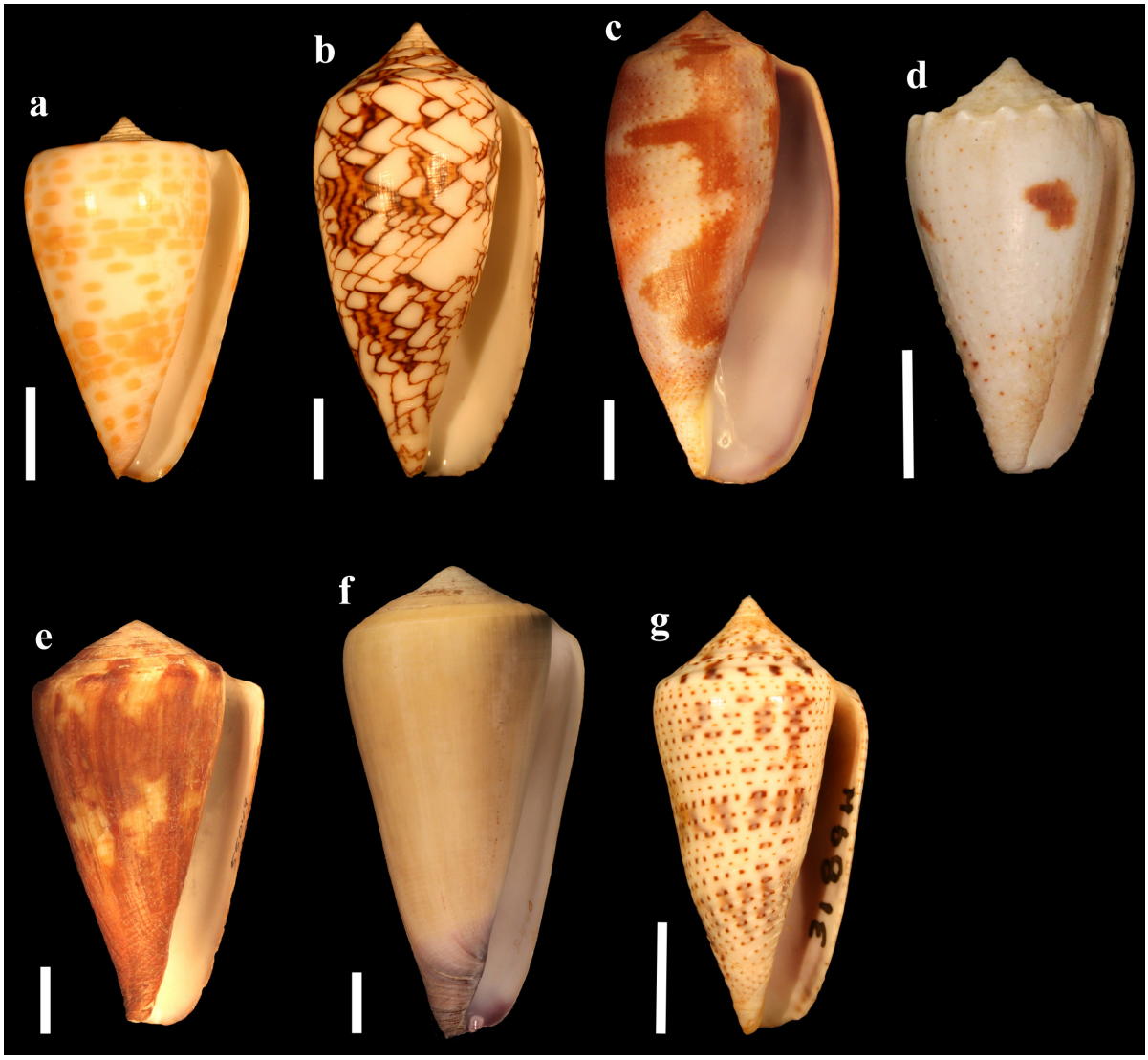
Figure A6: Scale bar is 1cm in each case.

a) *Conus tessulatus* PRI 13K
b) *C. textile* PRI 54455
c) *C. tulipa* CAS 179312
d) *C. varius* CAS 180467
e) *C. vexillum* CAS 178071
f) *C. virgo* CAS 180448
g) *C. ximenes* PRI 3189H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APPENDIX 2

NCBI GenBank Accession numbers for 16s and Calmodulin sequences.

Species	16s	Calmodulin
abbreviatus	AF174140	AF113252
anemone	AF174141	AF113253
araneosus	AF174142	AF113254
archon	AY381995	AY382035
arcuatus	AY381996	AY382036
balteatus	AF174146	AF113256
bandanus	AY381999	AF113257
brunneus	AF174149	AF113259
californicus	AF174151	AY382040
catus	AF174154	AF113260
chaldaeus	AF174155	AF113262
cinereus	AF174156	AF113263
coronatus	AF174160	AF113268
dalli	AY382004	AY382042
daucus	AY382005	AY382043
diadema	AY382006	AY382044
distans	AF174162	AF113270
dorreensis	AF174163	AF113271
ebraeus	AF174164	AF113272
eburneus	AF174165	AF113273
episcopatus	AF174167	AF113275
figulinus	AF160702	AF113276
flavidus	AF174168	AF113277
furvus	EU682301	AF113278
generalis	AF174170	AF113279
geographus	AF174171	AF113280
gladiator	AY382008	AY382047
imperialis	AF174173	AF113282
jaspideus	AY382030	AY382059
leopardus	AF174175	AF113284
litoglyphus	AF174176	AF113285
lividus	AF174178	AF113287
magus	AF174179	AF113288
mahogani	AY382014	AY382050
marmoreus	AF174180	AF113289
miles	AF174182	AF113291
miliaris	AF174181	AF113290
mus	AY382016	AY382052
musicus	AF174185	AF113294
nux	AF174186	AF113296
omaria	AF174188	AF113298
patricius	AY382021	AY382054
pennaceus	AF174190	AF113300
perplexus	AY382022	AY382055
planorbis	AF174191	AF113301
princeps	AF480307	AF113302
pulicarius	AF174194	AF113304
purpurascens	AF480308	AF480311
quercinus	AF174195	AF113305
rattus	AF174196	AF113306
regius	AF174197	AF113307
sponsalis	AF174199	AF113309
stercusmuscarum	AF174200	AF113310
striatus	AF174202	AF113311
tessulatus	AF174205	AF113315
textile	AF174206	AF113316
tulipa	AF174207	AF113317
varius	AF174208	AF113318
vexillum	AF174209	AF113320
virgo	AF174211	AF113319
ximenes	AY382033	AY382061

APPENDIX 3

Total evidence TNT matrix of *Conus* species for analyses presented in chapter 1.

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xread
'Chapter 1: Conus Total Evidence Dataset 61 taxa 678 characters'
678 61

&[cont]

abbreviatus
5.017-5.042 4.898-4.918 5.044-5.065 5.007-5.031
5.000-5.026 4.978-5.003 4.970-4.990 4.996-5.011
4.986-5.003 4.989-5.007 5.007-5.017 4.982-4.996
4.999-5.010 4.991-5.003

anemone
4.927-4.961 5.006-5.027 4.977-4.993 4.980-4.997
4.987-5.001 5.000-5.017 5.013-5.024 4.994-5.003
5.009-5.019 4.996-5.004 4.998-5.010 5.009-5.018
5.000-5.006 4.999-5.005

araneosus
5.033-5.061 4.973-4.998 4.923-4.937 4.982-4.995
4.973-4.993 4.973-4.995 4.998-5.013 4.986-5.008
4.995-5.013 4.981-4.997 4.993-5.009 5.009-5.022
4.994-5.004 5.001-5.017

archon
4.825-4.852 4.939-4.966 4.940-4.968 5.007-5.026
5.022-5.036 5.007-5.029 4.992-5.002 4.991-5.003
4.974-4.982 4.965-4.979 4.980-4.997 4.985-4.995
4.996-5.004 5.001-5.010

arcuatus
4.722-4.736 5.042-5.050 4.947-4.958 5.007-5.029
5.029-5.038 4.933-4.945 4.973-4.981 4.948-4.968
5.034-5.046 5.025-5.038 5.000-5.013 4.964-4.974
4.964-4.977 4.974-4.993

balteatus
5.045-5.072 4.927-4.954 4.970-4.983 4.972-4.995
4.939-4.957 4.953-4.972 4.999-5.016 5.017-5.033
5.001-5.014 4.996-5.004 4.987-5.005 4.993-5.006
4.990-5.004 4.991-5.001

bandanus

5.117-5.153	5.005-5.034	4.964-4.981	4.989-5.017
5.021-5.045	4.985-5.008	5.022-5.041	4.968-4.993
4.984-4.996	5.005-5.021	4.991-5.015	4.982-4.991
5.001-5.016	5.013-5.039		

brunneus

4.970-5.008	4.914-4.932	4.989-5.013	5.013-5.041
4.965-5.006	4.999-5.025	5.000-5.018	4.988-4.996
4.982-4.994	4.985-5.001	4.989-4.999	5.012-5.020
4.985-4.994	4.975-4.991		

californicus

4.923-4.937	4.979-4.990	5.056-5.075	4.963-4.981
4.972-4.986	4.972-4.983	5.003-5.016	4.988-5.000
4.992-5.002	4.989-4.999	4.993-5.005	4.988-4.995
5.002-5.009	4.994-5.002		

catus

4.978-4.997	4.984-5.000	5.017-5.031	4.987-5.004
4.977-4.990	4.983-4.996	4.999-5.014	5.009-5.025
5.007-5.016	5.005-5.015	4.986-4.993	5.007-5.016
5.007-5.017	4.986-4.994		

chaldaeus

4.968-4.993	4.915-4.930	5.095-5.109	4.963-4.992
4.998-5.011	4.992-5.008	5.006-5.022	4.992-5.009
5.007-5.025	4.984-4.999	4.991-5.004	4.990-5.009
4.976-4.986	4.998-5.012		

cinereus

4.964-4.975	5.100-5.109	4.941-4.954	4.992-5.005
4.995-5.004	5.026-5.034	5.017-5.031	5.007-5.015
5.021-5.028	5.009-5.018	4.997-5.004	4.985-4.996
5.005-5.013	4.991-4.997		

coronatus

4.937-4.963	4.933-4.944	5.052-5.069	5.007-5.025
4.994-5.016	4.990-5.000	4.984-4.995	5.005-5.014
4.993-5.008	4.995-5.013	4.996-5.010	5.012-5.025
5.001-5.017	5.002-5.016		

dalli

4.959-4.979	5.008-5.017	4.977-4.991	4.966-4.985
4.985-4.994	4.996-5.007	4.981-4.999	5.016-5.031

5.004-5.022	4.994-5.003	5.002-5.008	4.983-4.989
5.019-5.030	4.996-5.003		

daucus

5.039-5.061	4.979-4.998	4.913-4.932	4.974-5.004
4.987-5.004	4.994-5.005	4.994-5.006	4.986-5.009
4.989-5.002	5.010-5.019	4.981-4.990	5.005-5.018
4.980-4.995	4.996-5.009		

diadema

4.938-4.969	4.906-4.915	5.016-5.045	5.010-5.038
4.940-4.962	5.032-5.058	4.973-4.994	4.973-4.992
5.001-5.012	5.002-5.026	4.973-4.994	4.975-4.993
5.023-5.033	4.977-5.005		

distans

5.079-5.107	5.009-5.031	4.974-4.991	4.946-4.978
4.968-4.988	4.991-5.014	4.973-4.992	4.980-5.002
4.989-5.001	4.981-4.995	4.990-5.004	4.981-4.995
4.976-4.988	4.984-5.013		

dorreensis

4.865-4.877	5.027-5.043	5.075-5.087	4.979-4.993
5.054-5.084	4.913-4.953	4.993-5.013	5.015-5.028
4.993-5.006	5.011-5.032	4.981-5.000	5.002-5.018
5.016-5.035	5.005-5.019		

ebraeus

4.970-4.986	4.918-4.925	5.051-5.059	4.979-4.989
5.000-5.009	5.003-5.012	4.989-4.998	4.984-4.993
5.006-5.012	4.989-4.997	5.000-5.005	4.997-5.003
4.989-4.995	4.996-5.001		

eburneus

5.076-5.099	4.956-4.968	4.966-4.979	5.018-5.030
5.029-5.038	5.001-5.007	4.972-4.982	5.000-5.010
5.004-5.011	5.001-5.006	4.995-5.000	5.006-5.013
4.986-4.994	5.002-5.008		

episcopatus

4.955-4.964	5.135-5.145	5.015-5.026	4.951-4.964
4.970-4.978	5.011-5.020	5.017-5.029	5.008-5.016
4.960-4.970	4.999-5.006	4.987-4.990	4.992-5.001
4.990-4.995	4.988-4.993		

figulinus

5.017-5.034	4.972-4.985	4.976-4.994	5.010-5.025
5.035-5.045	5.003-5.011	4.990-5.005	5.024-5.034
5.023-5.030	5.007-5.012	4.997-5.005	4.983-4.994
5.003-5.013	4.999-5.003		

flavidus

5.088-5.105	4.994-5.022	5.003-5.025	4.933-4.976
4.987-5.001	4.997-5.010	4.981-4.996	4.974-5.000
4.973-4.983	4.984-4.990	4.982-5.002	5.001-5.010
4.988-4.996	4.988-5.001		

furvus

4.990-5.019	5.028-5.041	4.907-4.920	4.962-4.981
4.968-4.987	4.987-5.004	4.991-5.010	5.006-5.020
5.001-5.009	4.988-4.998	4.991-5.002	5.005-5.013
4.999-5.006	5.006-5.015		

generalis

4.932-4.945	4.992-4.999	4.842-4.849	5.013-5.017
4.978-4.984	5.030-5.034	4.995-4.998	4.994-4.997
4.970-4.975	4.999-5.001	4.992-4.994	5.015-5.017
4.983-4.985	5.009-5.011		

geographus

4.977-4.987	5.174-5.180	5.061-5.074	5.065-5.077
4.930-4.940	4.995-5.003	4.977-4.991	5.000-5.010
5.045-5.052	4.973-4.985	5.039-5.052	4.997-5.009
5.007-5.019	5.002-5.014		

gladiator

5.074-5.098	4.969-4.982	4.957-4.973	5.018-5.037
4.984-4.999	4.977-4.998	4.989-5.005	4.981-4.996
5.005-5.015	4.992-5.002	5.003-5.015	4.992-5.000
5.002-5.009	4.993-4.998		

imperialis

5.169-5.188	5.016-5.042	5.042-5.064	5.011-5.065
4.982-5.021	4.986-5.011	5.006-5.046	5.001-5.022
4.999-5.007	4.988-5.008	4.963-4.992	4.994-5.006
4.990-5.017	5.013-5.039		

jaspideus

4.778-4.792	5.039-5.047	5.005-5.015	4.996-5.014
5.023-5.033	4.923-4.944	4.978-4.995	4.984-5.000

4.992-5.001	5.025-5.057	4.977-5.006	4.996-5.008
4.988-4.999	4.999-5.011		

leopardus

5.155-5.167	5.003-5.015	5.059-5.071	5.006-5.045
4.989-5.012	4.992-5.002	4.978-5.015	4.991-5.007
4.959-4.971	4.992-5.002	4.979-4.993	4.982-4.993
4.985-4.992	4.995-5.005		

lithoglyphus

5.103-5.125	5.045-5.064	4.948-4.969	4.978-4.999
5.017-5.027	5.005-5.017	4.978-4.994	4.965-4.975
5.003-5.017	4.996-5.003	4.990-4.997	5.006-5.014
4.991-4.999	4.997-5.003		

lividus

5.043-5.071	4.965-4.980	4.988-5.001	4.968-4.989
4.963-4.981	4.971-4.985	4.987-5.001	4.973-4.984
4.984-4.996	4.988-5.004	4.997-5.004	4.995-5.006
5.001-5.013	4.983-5.001		

magus

5.029-5.043	5.084-5.101	4.983-4.994	4.998-5.009
5.013-5.022	5.016-5.024	4.993-5.002	5.000-5.007
4.981-4.989	4.999-5.007	4.995-5.000	4.993-4.998
4.997-5.005	4.987-4.993		

mahogani

4.813-4.828	5.034-5.045	4.948-4.957	4.997-5.005
4.995-5.006	4.992-5.003	4.982-4.992	4.993-5.001
4.974-4.984	4.956-4.965	4.980-4.995	4.986-4.993
5.011-5.020	4.996-5.004		

marmoreus

5.110-5.129	5.011-5.029	4.977-4.992	4.949-4.964
5.020-5.040	4.983-5.001	5.029-5.045	4.990-5.012
4.996-5.007	4.989-5.007	5.008-5.029	4.990-4.998
5.003-5.017	4.993-5.007		

miles

5.023-5.043	4.951-4.961	4.997-5.008	4.975-4.986
4.968-4.977	4.992-5.002	4.998-5.005	4.990-4.997
4.986-4.996	4.997-5.001	5.005-5.010	4.981-4.987
4.998-5.005	4.991-4.996		

miliaris

4.997-5.025	4.872-4.889	5.040-5.058	4.999-5.017
5.017-5.039	4.988-5.014	4.973-4.989	4.999-5.016
4.998-5.011	4.993-5.005	4.989-4.999	4.994-5.005
4.999-5.009	5.008-5.023		

mus

4.895-4.920	4.934-4.941	5.001-5.015	5.002-5.016
4.985-5.001	4.999-5.014	5.016-5.029	4.983-4.994
5.007-5.019	4.987-5.005	4.993-5.003	4.993-5.000
4.977-4.985	4.991-4.997		

musicus

5.054-5.085	4.960-4.972	5.005-5.029	4.945-4.982
4.985-4.994	4.962-4.989	4.967-4.976	4.980-4.993
4.982-4.993	5.001-5.009	4.991-4.999	5.004-5.014
4.992-5.003	5.002-5.012		

nux

5.008-5.056	4.923-4.939	5.030-5.064	5.011-5.048
4.973-4.990	4.959-4.988	4.973-4.991	4.973-4.989
4.992-5.013	4.992-4.998	5.009-5.015	4.987-5.008
4.966-4.988	4.985-5.013		

omaria

4.978-5.002	5.106-5.126	5.031-5.046	4.956-4.971
4.970-4.983	5.007-5.013	4.994-5.015	4.994-5.014
4.979-4.992	4.991-5.003	4.991-5.000	5.002-5.011
4.986-4.995	5.002-5.005		

patricius

5.023-5.045	4.986-4.997	4.935-4.958	5.005-5.024
5.020-5.029	5.010-5.014	5.009-5.021	5.008-5.020
5.056-5.068	5.002-5.008	5.006-5.012	4.954-4.961
4.987-4.995	4.991-4.995		

pennaceus

4.986-4.997	5.022-5.049	5.011-5.019	4.965-4.983
4.987-4.998	4.994-5.001	5.014-5.021	5.006-5.018
4.981-4.991	5.006-5.013	4.986-4.993	4.998-5.009
5.004-5.010	4.992-4.998		

perplexus

4.905-4.920	4.943-4.952	4.981-4.992	5.029-5.041

5.024-5.039	5.042-5.050	4.983-4.995	5.007-5.016
4.996-5.004	4.976-4.987	4.996-5.002	4.998-5.004
5.010-5.015	5.000-5.005		

planorbis

5.118-5.129	5.030-5.046	4.973-4.987	5.005-5.023
5.021-5.029	4.986-4.998	4.972-4.985	4.965-4.984
4.984-4.998	4.990-4.996	4.992-4.997	5.008-5.016
4.993-5.006	4.995-5.003		

princeps

5.113-5.129	5.001-5.014	4.987-4.999	4.997-5.021
4.993-5.005	4.983-4.992	5.014-5.023	4.977-4.989
5.004-5.018	5.006-5.012	4.991-4.997	4.990-5.003
4.988-4.996	4.997-5.007		

pulicarius

5.023-5.045	4.962-4.975	4.993-5.004	4.985-4.998
5.048-5.061	4.984-4.995	4.995-5.007	5.032-5.043
4.983-4.994	5.001-5.013	5.004-5.018	5.038-5.049
5.010-5.018	4.995-5.008		

purpurascens

5.016-5.038	4.965-4.984	4.992-5.003	4.985-4.996
4.971-4.980	4.983-4.999	5.001-5.013	5.008-5.022
5.006-5.020	4.991-4.998	5.003-5.012	4.998-5.011
5.018-5.025	4.992-5.001		

quercinus

4.966-5.008	4.923-4.937	4.933-4.947	5.031-5.039
5.010-5.017	5.019-5.025	4.980-4.991	5.004-5.013
4.991-5.003	4.990-4.998	4.999-5.004	4.997-5.004
4.992-5.001	4.997-5.002		

rattus

5.043-5.056	4.950-4.963	4.990-5.000	4.981-4.992
4.965-4.973	4.979-4.987	4.997-5.007	4.975-4.987
4.998-5.004	5.001-5.006	5.011-5.016	4.982-4.990
5.013-5.019	4.992-4.998		

regius

4.896-4.947	4.913-4.936	4.980-5.015	4.982-5.007
4.968-4.988	5.020-5.038	5.043-5.064	4.991-5.014
4.988-5.007	4.981-5.007	4.982-5.004	4.990-5.009
4.974-4.991	4.994-5.006		

sponsalis

5.000-5.020	4.893-4.909	5.051-5.064	5.010-5.044
4.990-5.002	4.958-4.970	4.970-5.003	4.985-5.000
4.974-4.987	5.002-5.009	5.002-5.011	4.983-4.994
4.990-4.998	4.985-4.995		

stercusmuscarum

5.008-5.019	5.101-5.109	5.046-5.060	4.989-5.009
5.014-5.023	5.011-5.027	4.984-5.001	5.004-5.016
4.957-4.962	5.006-5.023	4.978-4.991	5.016-5.028
4.988-4.996	4.988-4.997		

striatus

4.994-5.001	5.124-5.131	5.033-5.043	5.006-5.020
5.002-5.011	5.028-5.036	4.953-4.964	4.998-5.012
4.989-4.998	4.994-5.006	4.984-4.993	5.004-5.009
4.979-4.986	4.999-5.004		

tessulatus

5.078-5.092	4.985-4.992	4.945-4.955	5.029-5.036
5.028-5.034	5.006-5.010	4.989-4.996	5.008-5.014
5.011-5.018	5.008-5.012	4.989-4.991	5.007-5.011
4.984-4.989	5.004-5.006		

textile

4.944-4.947	5.042-5.044	4.971-4.972	4.998-5.001
4.987-4.988	4.994-4.995	5.014-5.016	5.011-5.012
4.995-4.996	5.006-5.007	5.000-5.001	5.006-5.007
5.013-5.014	4.999-5.000		

tulipa

4.964-4.974	5.133-5.141	5.027-5.038	5.053-5.064
4.943-4.950	4.996-5.004	5.000-5.009	4.996-5.007
5.047-5.057	4.982-4.987	5.025-5.032	4.995-5.001
4.996-5.006	5.007-5.013		

varius

5.055-5.079	4.968-4.997	4.970-4.993	4.968-4.983
4.956-4.980	4.978-5.007	5.005-5.024	4.983-4.993
4.998-5.008	4.980-5.011	4.997-5.018	4.953-4.967
5.000-5.014	4.978-4.992		

vexillum

5.060-5.075	4.975-4.990	4.975-4.988	4.969-4.983

4.962-4.974	4.987-4.998	5.006-5.023	4.981-4.996
5.000-5.006	4.993-4.998	5.004-5.011	4.956-4.963
5.002-5.012	4.983-4.987		

virgo

5.101-5.115	5.054-5.072	4.974-4.986	4.935-4.958
4.999-5.010	5.009-5.021	5.005-5.017	4.987-5.004
4.973-4.983	4.995-5.001	4.989-4.995	4.990-5.000
4.990-4.999	4.989-4.997		

ximenes

4.874-4.899	5.014-5.025	4.935-4.947	5.015-5.027
4.990-5.011	5.022-5.034	4.995-5.010	4.999-5.008
4.988-4.999	4.968-4.991	5.003-5.016	4.994-5.003
5.010-5.016	5.006-5.012		

&[dna]

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anemone

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araneosus

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archon

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bandanus

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brunneus

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californicus

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catus

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chaldaeus

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cinereus

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coronatus

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daucus

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diadema

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dorreensis

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figulinus

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flavidus

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furvus

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generalis

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geographus

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gladiator

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imperialis

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jaspideus

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leopardus

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lithoglyphus

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lividus

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magus

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mahogani

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marmoreus

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miles

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miliaris

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mus

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musicus

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nux

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omaria

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patricius

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pennaceus

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perplexus

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planorbis

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princeps

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pulicarius

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purpurascens

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quercinus

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rattus

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regius

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sponsalis

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stercusmuscarum

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G?

striatus

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tessulatus

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textile

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A?

tulipa

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varius

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vexillum

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ACG?

virgo

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ximenes

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CCAGGCAACGGCACCATTGACTTCCCCGAGTTCCTGACG?

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APPENDIX 4

Stiracolpus TNT matrix. Pages 217-257 contain the character data. Pages 258-265 contain weighting code for the various analyses presented in chapter 2. To run a weighted analysis, one of the Ccode blocks should be appended to the end of the character code after the last semicolon.

nstates cont;
xread
'Chapter 2: Stiracolpus: 21 eigenaxes.'
346 24

&[cont]

m_roseus 2.5-4 8.7 2.5 18

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4.987-5.026 5.017-5.033 4.972-5.021 4.997-5.057 4.967-4.979
5.027-5.036

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4.995-5.020

4.928-5.027 4.830-4.971 4.846-4.951 4.904-5.013 5.047-5.082
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4.980-5.015 5.054-5.069 5.043-5.073 4.966-5.045 4.989-5.045
5.001-5.017 4.983-5.007 4.968-5.030 4.991-5.029 5.008-5.039
5.001-5.002

4.927-4.942 4.816-4.896 4.811-4.915 4.882-4.907 5.054-5.098
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4.983-5.010 5.002-5.063 5.048-5.072 4.996-5.049 4.964-5.006
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4.989-5.008

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4.997-5.021 4.951-5.002 4.993-5.010 4.988-5.029 4.959-5.007
4.997-5.043 5.010-5.036 4.967-4.998 4.977-4.993 4.986-5.024
4.983-5.021

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5.038-5.044

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4.999 5.016 4.904 5.009 4.982 4.998 4.996 5.034 5.057 5.046
5.021

s_ahiparanus 1.25 2.33 0.7 13

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4.994-5.033	4.967-5.004	4.935-4.999	4.963-5.010	4.962-4.996
5.017-5.035				

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4.986-5.001				

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4.979-5.013	4.972-4.995	5.001-5.053	4.975-5.018	4.986-5.010
4.994-5.023				

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4.993-5.039	4.989-5.049	5.020-5.049	4.981-5.032	5.004-5.043
4.994-5.024	4.995-5.036	5.002-5.051	4.970-5.001	4.957-4.988
5.002-5.028				

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4.963-4.998	4.968-4.993	4.984-5.051	4.964-4.997	4.975-5.026
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4.998-5.011				

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5.056-5.081	4.967-5.013	4.954-4.989	4.981-5.011	4.963-5.021
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4.946-4.983	4.968-4.987	4.968-5.000	5.023-5.062	4.973-5.006
4.967-4.987				

5.038-5.076	5.035-5.068	5.145-5.170	4.883-4.914	5.040-5.064
5.042-5.101	5.003-5.034	4.978-4.998	4.954-4.995	4.955-4.988
4.931-4.970	4.989-5.023	4.947-4.985	4.985-5.005	4.956-4.970
4.974-4.991	5.002-5.039	4.969-5.011	4.991-5.027	5.006-5.029
4.991-5.013				

5.059-5.100	4.981-5.041	5.109-5.136	4.895-4.920	5.027-5.040

5.039-5.064 4.983-5.042 4.989-5.015 4.993-5.023 4.973-4.989
4.945-4.970 5.009-5.032 4.972-4.985 5.017-5.038 4.959-4.981
4.986-5.007 4.979-5.014 4.996-5.005 4.983-5.013 4.983-5.016
4.980-5.011

5.047-5.085 5.010-5.046 5.097-5.123 4.898-4.930 5.016-5.049
5.032-5.050 4.987-5.017 4.981-5.003 5.010-5.034 4.995-5.018
4.953-4.982 5.005-5.035 4.979-5.004 5.023-5.062 4.978-5.008
5.002-5.037 5.006-5.019 4.977-5.011 5.026-5.048 4.998-5.019
5.002-5.046

5.019-5.055 4.964-5.037 5.092-5.123 4.955-5.012 5.002-5.034
5.004-5.036 4.953-5.015 4.950-5.010 5.001-5.061 5.004-5.024
4.945-4.976 5.001-5.036 4.980-4.999 4.968-4.995 4.955-4.979
4.991-5.017 4.991-5.042 4.974-4.999 5.004-5.044 4.997-5.011
4.995-5.012

4.983-5.070 4.994-4.995 4.995-5.090 4.916-5.114 5.015-5.043
5.000-5.085 4.950-5.073 4.881-5.036 5.036-5.045 4.924-5.041
4.904-4.922 5.050-5.086 4.968-5.010 5.023-5.039 4.992-5.055
4.991-5.035 4.979-5.015 4.991-5.032 4.959-5.002 5.027-5.048
4.977-5.034

5.092 5.050 5.103 4.988 5.043 5.008 4.958 4.992 5.028 5.000
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4.991-5.035 4.934-4.980 5.039-5.072 5.048-5.108 4.917-4.955
5.033-5.087 4.968-5.015 4.956-4.988 4.972-5.014 4.977-5.022
4.999-5.021 5.006-5.027 5.005-5.023 4.991-5.021 4.963-4.983
4.989-5.004 5.004-5.019 4.992-5.003 4.987-5.001 4.991-5.002
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4.899-4.950 5.023-5.063 5.055-5.104 4.958-4.997 4.987-5.030

5.006-5.021 4.996-5.035 4.988-5.025 4.964-4.998 4.993-5.029
4.999-5.024 5.010-5.048 4.964-4.998 4.993-5.012 4.993-5.020
4.990-5.010 4.984-5.015 4.982-5.005 4.998-5.009 5.009-5.036
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5.005-5.039 5.017-5.054 5.019-5.046 4.960-4.986 4.998-5.020
5.047-5.088 4.978-5.002 5.016-5.034 4.938-4.963 4.996-5.019
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5.028-5.152 5.050-5.100 4.914-4.971 5.045-5.076 4.916-4.974
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4.997-5.043 5.016-5.055 4.993-5.029 5.011-5.048 4.965-4.994
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4.971-5.003 4.956-5.012 4.967-5.017 4.981-5.051 4.964-5.028
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4.993-5.034

5.248 4.930 4.939 5.110 5.039 5.015 5.033 5.005 5.017 4.983
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5.116 5.032 5.016 4.991 4.958 4.945 5.034 4.942 5.037 5.025
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4.915 5.005 5.063 4.951 5.028 5.061 5.050 5.035 4.921 5.054
4.995 4.914 4.963 5.043 4.926 4.942 5.048 5.031 4.960 5.002
5.014

4.988 4.912 5.129 5.090 4.964 4.948 5.036 5.055 4.860 4.829
5.113 5.009 4.992 5.069 4.941 4.883 5.046 4.969 4.997 4.995
5.063

4.942 5.060 4.972 4.902 4.876 4.923 5.047 4.958 4.992 5.051
4.968 5.049 5.019 5.016 4.957 4.977 4.932 5.024 5.013 5.108
4.958

4.947 5.126 4.854 5.068 4.995 4.975 4.882 4.959 5.068 4.958
4.972 4.984 5.039 4.971 4.957 4.986 5.012 5.029 5.021 5.004
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5.095 5.147 4.972 4.968 4.958 4.953 5.048 4.981 4.977 5.067
4.952 5.028 4.983 4.958 4.894 5.052 4.944 5.034 5.022 5.072
5.031

5.114 4.885 5.025 4.994 4.832 4.843 5.079 5.019 4.892 4.997
4.937 5.025 4.975 5.020 4.925 4.981 5.108 5.040 5.008 4.983
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5.139 5.126 4.969 5.017 4.960 4.919 5.025 4.950 4.886 5.049
4.947 4.952 4.965 4.999 4.889 4.991 5.067 5.003 4.994 5.020
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5.151 5.120 4.938 4.999 4.989 4.957 4.996 4.983 4.921 5.076
4.996 4.995 5.022 5.031 4.986 5.010 5.053 5.064 5.023 4.977
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5.185 5.109 4.961 5.005 4.951 4.907 5.022 4.991 4.929 5.059
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4.828-4.954 4.904-4.979 5.091-5.120 4.995-5.095 4.903-4.928
5.036-5.094 4.989-5.081 5.017-5.054 4.997-5.050 4.996-5.039
4.957-4.982 5.013-5.047 4.967-5.012 5.006-5.043 4.972-4.985
4.963-4.993 5.002-5.015 4.991-5.054 4.982-4.992 4.989-5.019
5.005-5.029

4.835-5.043 4.908-5.061 5.008-5.082 5.032-5.128 4.949-5.037
4.958-5.038 4.929-5.011 4.947-5.021 4.996-5.077 4.969-5.024
4.958-5.042 4.978-5.036 4.973-5.019 4.989-5.011 5.007-5.068
4.962-5.023 4.981-5.016 4.947-4.987 4.970-5.003 4.979-5.031
4.971-4.997

4.854-5.022 4.964-5.031 5.046-5.083 4.987-5.062 4.944-4.993
4.932-4.979 4.916-4.999 4.902-4.992 4.985-5.043 4.939-4.987
4.999-5.032 4.971-5.017 4.975-5.003 4.935-4.978 5.014-5.054
5.018-5.060 4.975-4.996 4.968-5.001 4.970-5.008 4.963-4.981

5.006-5.029

4.815-4.942	5.044-5.162	4.937-5.016	4.991-5.039	4.922-5.017
4.993-5.079	4.909-4.948	4.944-4.987	5.026-5.064	4.968-5.022
4.983-5.032	4.960-4.980	4.947-5.022	4.965-5.022	4.968-5.025
4.928-4.990	4.988-5.041	4.961-5.012	4.981-5.005	4.972-5.040
4.974-5.004				

4.934-5.046	5.066-5.176	4.953-5.007	4.984-5.034	4.963-5.036
4.935-5.010	4.931-4.990	5.007-5.071	4.985-5.040	4.953-4.997
5.003-5.030	4.979-5.052	4.951-4.984	4.928-4.991	4.974-5.012
4.973-5.006	4.991-5.020	4.963-5.002	5.032-5.063	5.004-5.036
4.992-5.025				

4.920-5.029	5.025-5.153	4.952-5.040	4.977-5.009	4.938-4.989
4.943-5.006	4.963-4.997	5.003-5.047	5.047-5.084	4.972-5.026
4.963-5.022	4.954-5.023	4.991-5.029	4.960-4.989	4.990-5.026
4.936-4.990	4.960-5.016	4.991-5.040	4.979-5.022	4.968-4.987
4.970-5.016				

4.947-5.118	5.105-5.194	4.919-4.975	4.990-5.023	4.960-5.000
4.886-4.981	4.939-5.015	5.026-5.057	5.010-5.031	4.973-5.000
4.970-5.024	4.944-4.984	4.986-5.038	4.987-5.026	4.967-4.989
4.986-5.024	4.976-5.027	4.955-4.998	4.989-5.033	4.954-4.995
4.959-4.983				

4.982-5.124	5.051-5.122	4.859-4.890	4.972-5.024	4.927-4.977
4.938-5.004	4.975-5.013	5.009-5.064	5.040-5.095	4.988-5.032
5.002-5.048	4.976-5.017	4.965-5.025	5.036-5.070	4.990-5.025
4.979-5.021	4.984-5.011	4.971-5.026	4.948-4.985	4.967-5.007
4.955-4.967				

4.925-5.137	4.975-5.076	4.902-4.971	4.951-5.033	4.913-4.962
4.910-4.965	4.992-5.042	5.028-5.090	4.950-5.016	5.016-5.044
5.022-5.065	4.988-5.065	5.010-5.046	4.991-5.073	4.973-4.998
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4.996-5.044	4.988-5.060	5.016-5.044	4.960-5.041	4.965-5.005
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5.004-5.040 5.019-5.072 5.038-5.083 4.978-5.015 4.998-5.018
4.962-5.002 4.982-5.048 4.984-5.051 4.913-4.952 4.993-5.029
5.006-5.031 4.985-4.991 4.985-5.001 4.998-5.021 4.996-5.029
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5.085-5.237 5.048-5.118 4.835-4.903 5.012-5.106 4.994-5.065
5.041-5.074 5.003-5.046 5.046-5.074 4.989-5.042 4.938-5.008
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4.911-4.958 4.773-5.057 5.013-5.162 4.967-5.036 5.073-5.170
5.004-5.005 4.901-5.024 4.838-5.052 5.007-5.036 5.002-5.025
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4.705-4.964 4.820-5.139 4.888-5.159 4.976-5.066 4.977-5.018
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4.693-4.794 4.865-4.973 4.980-5.085 4.952-5.025 4.866-4.943

4.878-4.918 5.024-5.141 5.030-5.074 4.996-4.998 4.991-5.034
4.944-5.016 4.975-4.985 4.986-5.013 4.982-5.033 4.961-5.079
4.938-5.013 4.965-5.004 4.996-5.012 4.975-5.018 4.990-5.032
4.979-5.009

4.703-4.815 4.816-5.071 4.943-4.995 4.951-5.027 4.946-5.000
4.947-4.954 4.953-5.025 5.017-5.026 4.995-5.066 5.009-5.120
4.978-5.002 4.956-4.961 4.981-5.007 4.914-5.016 4.983-5.028
5.003-5.067 4.946-5.064 4.926-4.978 4.924-4.997 4.991-5.006
5.014-5.106

4.758-4.814 5.035-5.045 4.834-4.914 4.859-4.986 4.923-5.008
4.900-5.065 4.979-5.033 4.991-5.042 4.977-5.001 4.993-5.005
4.981-5.029 4.912-4.977 4.972-4.979 4.967-5.001 4.972-5.048
4.946-5.018 5.071-5.110 4.999-5.019 4.996-5.022 4.931-4.975
4.996-4.997

4.826-4.925 5.104-5.118 4.814-4.899 4.915-4.980 4.795-4.971
4.951-5.008 4.948-5.066 4.984-4.991 4.990-5.012 4.986-5.051
4.944-4.972 4.978-5.011 4.903-4.986 4.951-5.073 4.967-4.985
4.954-4.994 4.919-4.976 4.986-5.064 4.976-5.049 4.985-5.022
4.918-4.995

4.984 5.140 4.831 4.928 4.969 5.034 4.960 4.972 5.023 5.001
5.014 4.990 4.937 4.964 4.971 5.037 4.949 4.993 4.947 5.034
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4.810 5.213 4.839 4.968 4.975 4.902 4.986 5.021 4.985 4.959
4.953 5.026 5.002 4.979 5.017 5.047 4.994 5.035 5.059 4.981
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5.122 5.229 4.858 5.013 4.972 4.951 4.998 4.963 4.977 4.996
5.014 5.018 4.970 5.029 5.023 4.980 5.029 5.042 5.021 4.981
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5.193 5.181 4.817 5.005 5.022 4.989 4.952 5.014 4.966 5.022
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5.059 4.887 4.974 4.882 4.887 5.000 4.826 4.945 4.972 4.843
5.047 4.998 5.024 5.116 5.011 4.987 4.974 5.072 5.016 4.991
5.026

5.129-5.217 4.838-4.887 4.935-4.999 4.886-4.979 4.911-4.935
4.905-5.000 4.943-4.961 5.014-5.044 4.974-5.057 5.057-5.076
4.914-5.015 4.951-5.068 4.892-5.013 5.014-5.078 4.975-5.049
4.933-5.080 4.993-5.034 4.921-4.973 4.968-4.986 5.036-5.055
4.991-5.050

5.052-5.121 4.690-4.823 4.787-4.869 4.943-5.064 4.884-4.990
4.931-4.958 4.951-4.987 4.992-5.044 4.974-5.006 5.082-5.088
4.995-5.060 5.057-5.076 4.873-4.883 4.947-4.975 5.046-5.082
4.964-5.023 4.979-5.006 4.904-5.031 4.946-5.000 4.951-4.970
4.968-4.975

5.033-5.133 4.726-4.793 4.850-4.978 4.948-4.984 4.922-4.983
5.006-5.071 4.976-5.007 4.974-5.098 4.972-5.057 4.939-5.015
5.018-5.049 5.004-5.040 4.972-5.039 4.981-5.007 4.936-5.005
4.924-4.957 4.973-5.000 4.944-4.974 4.987-5.004 4.988-5.016
4.966-5.027

4.948-5.001 4.673-4.907 4.958-5.068 4.872-4.939 4.904-4.983
4.957-5.040 4.916-4.998 4.918-4.986 5.048-5.063 4.977-5.069
5.015-5.117 4.992-5.133 4.975-5.010 4.988-5.080 4.949-5.012
4.965-5.039 4.908-4.968 5.030-5.076 4.937-4.982 4.887-5.009
4.924-4.977

4.983-5.087 4.776-4.834 4.966-4.987 4.823-4.927 4.946-4.966
4.876-4.955 4.868-4.971 4.882-5.015 4.931-4.976 4.889-4.968

4.935-5.000 4.992-5.025 5.018-5.067 4.998-5.035 4.953-4.996
4.943-5.042 5.014-5.026 4.957-5.031 4.984-5.056 5.012-5.026
4.964-5.035

5.051-5.032 4.847-4.769 4.998-4.942 4.868-4.855 4.966-4.911
5.031-4.950 4.933-4.863 4.966-4.904 5.050-4.969 4.995-4.929
5.037-4.982 5.040-5.013 4.977-4.894 5.051-4.961 5.022-5.004
5.055-5.003 5.063-5.034 5.005-4.967 5.062-5.048 5.047-4.980
5.008-4.995

5.000-5.075 4.738-4.836 4.969-4.993 4.823-5.004 4.923-5.002
4.991-4.999 4.859-4.980 4.925-4.957 4.975-5.022 4.944-4.956
4.975-5.040 5.029-5.098 4.880-4.989 5.015-5.042 4.992-5.051
4.980-5.069 4.969-5.007 4.949-4.991 4.923-5.064 4.961-4.978
5.005-5.113

5.026 4.878 4.955 4.943 4.952 4.928 4.797 4.951 4.992 4.918
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5.013-5.017 5.033-5.033 5.101-5.102 5.038-5.227 4.732-4.853
5.067-5.080 4.921-4.963 4.992-5.011 4.984-5.028 5.031-5.080
5.030-5.034 4.976-4.994 5.003-5.069 4.998-5.044 4.978-5.013
4.941-5.030 4.994-5.044 4.943-4.968 4.993-4.997 4.973-4.993
4.994-4.995

4.843-5.179 5.076-5.087 5.002-5.016 4.973-5.045 4.819-4.922
5.048-5.081 4.996-5.084 4.869-4.945 5.033-5.079 5.061-5.093
4.936-4.984 4.995-5.020 5.022-5.047 4.957-5.007 4.963-4.991

4.971-5.018	4.992-5.005	5.070-5.079	4.986-5.005	4.994-5.036
4.992-5.010				
4.691-4.943	4.972-5.169	4.847-5.084	5.005-5.045	4.808-5.063
4.945-5.136	4.973-5.009	5.067-5.083	4.883-4.984	4.852-5.056
4.891-4.940	4.943-5.052	4.997-5.068	4.966-5.026	4.956-5.053
4.945-4.957	4.986-4.997	4.982-4.992	5.006-5.022	5.003-5.038
4.949-5.025				
4.688-4.736	4.872-4.928	5.027-5.126	4.842-4.969	4.882-4.936
4.931-4.980	5.026-5.067	5.001-5.129	4.926-5.024	4.884-4.994
5.007-5.084	4.927-4.949	4.985-5.028	5.025-5.095	4.956-5.019
4.949-5.110	4.909-4.963	4.996-5.054	4.984-5.007	5.029-5.043
4.970-5.043				
4.683-4.787	4.921-5.023	4.914-5.016	4.860-4.905	4.953-4.966
4.968-5.039	4.996-5.034	4.964-5.009	4.909-5.081	4.972-5.043
4.998-5.014	4.953-4.980	4.977-5.032	4.941-5.011	5.010-5.049
4.929-4.985	5.006-5.031	5.031-5.049	5.003-5.012	5.005-5.022
4.988-5.035				
4.726-4.762	4.978-5.013	4.852-4.881	4.899-4.943	4.968-5.000
4.944-4.972	4.939-4.986	4.974-5.026	4.995-5.044	5.027-5.069
4.884-4.972	4.969-5.012	5.001-5.032	4.912-4.963	4.958-5.020
4.942-4.990	4.913-5.002	4.982-5.019	5.023-5.072	4.963-5.038
4.913-4.997				
4.778-4.808	4.934-4.971	4.890-4.903	4.911-4.938	4.940-4.982
4.900-4.933	4.988-5.071	4.959-4.969	4.990-5.076	4.938-5.003
4.919-4.974	4.921-4.942	4.983-5.059	4.947-4.963	4.952-5.013
4.981-5.004	4.966-5.051	4.987-5.019	4.914-4.959	4.975-5.022
4.948-4.987				
4.725-4.779	4.896-4.987	4.857-4.961	4.926-4.933	4.968-5.012
4.929-4.981	4.995-5.032	4.846-4.972	5.036-5.086	5.007-5.017
4.939-4.976	4.994-5.001	5.025-5.072	4.900-4.949	4.969-5.047
4.955-5.014	4.923-5.016	5.009-5.017	4.950-5.040	4.994-5.052
4.984-4.998				
4.727-4.904	4.945-5.086	4.878-4.939	4.925-4.985	4.997-4.998
4.871-4.937	4.993-5.015	4.916-4.952	5.036-5.084	4.895-5.016
4.897-4.986	4.973-5.002	4.992-5.026	4.974-5.017	4.907-5.021
5.019-5.055	5.007-5.066	4.999-5.040	4.886-5.025	5.012-5.013
4.991-5.046				

4.810-4.847 4.893-4.994 4.872-4.967 4.868-5.059 5.006-5.060
4.961-4.988 5.011-5.061 4.833-4.949 5.020-5.021 4.918-5.059
4.865-4.886 4.901-5.015 4.966-5.035 5.001-5.018 4.968-5.097
4.975-5.010 4.911-4.978 4.929-4.994 4.953-4.980 4.969-5.004
4.905-4.970

4.857-4.998 5.005-5.068 4.808-4.932 4.843-5.014 5.033-5.052
4.882-4.931 5.035-5.043 4.932-5.036 4.896-5.045 4.890-4.962
4.917-4.985 4.974-5.033 4.913-5.095 4.986-5.030 4.993-5.002
4.975-5.074 4.982-5.019 4.994-5.003 4.937-5.003 4.973-5.049
5.020-5.040

4.879 5.005 4.933 4.954 5.032 4.888 5.046 4.912 5.048 4.917
4.964 5.011 4.987 4.988 4.958 5.007 4.992 4.953 4.989 4.956
5.040

4.910 4.918 4.971 4.987 4.994 5.040 5.026 4.894 5.049 5.005
4.952 4.995 4.974 4.992 5.025 5.010 5.039 4.995 5.037 5.047
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4.928-5.073 4.954-5.069 4.974-5.081 5.066-5.158 4.868-4.902
5.013-5.096 4.957-5.023 4.951-5.035 4.955-4.990 4.984-5.019
5.000-5.028 4.960-4.991 4.990-5.022 5.007-5.025 4.998-5.007
4.998-5.026 4.976-4.994 5.002-5.032 4.993-5.014 5.002-5.016
4.982-5.010

4.794-4.880 5.109-5.212 5.067-5.152 5.029-5.141 4.996-5.093
4.959-5.048 4.938-5.063 4.924-4.983 5.022-5.094 4.989-5.088
4.964-5.014 4.999-5.046 4.942-4.987 5.006-5.049 4.996-5.048
4.982-5.001 4.945-4.987 4.988-5.022 4.985-5.012 4.994-5.013
4.999-5.004

4.689-4.799 5.025-5.137 5.000-5.092 5.048-5.132 4.967-5.033
4.994-5.057 5.009-5.084 4.992-5.060 4.979-5.041 4.926-5.020
4.893-4.963 4.976-5.010 4.929-4.987 5.018-5.061 4.984-5.043
4.984-5.008 4.991-5.018 4.971-5.027 4.975-5.032 4.967-5.019

4.987-5.016

4.701-4.757	5.047-5.178	4.974-5.034	5.075-5.137	5.047-5.123
4.911-4.952	4.882-4.960	5.046-5.074	5.030-5.068	4.964-5.016
4.966-5.024	5.008-5.063	4.940-5.011	5.053-5.096	5.025-5.047
4.984-5.027	4.987-5.017	4.945-4.994	4.971-5.009	4.990-5.011
4.987-5.015				

4.678-4.754	5.018-5.071	5.023-5.044	5.110-5.151	5.074-5.122
4.931-4.997	4.939-4.981	5.044-5.092	4.969-5.051	4.968-5.031
4.912-4.993	4.970-5.034	4.999-5.044	4.950-5.003	4.941-4.984
4.955-5.001	4.957-5.017	4.951-5.019	4.964-5.016	4.982-5.055
5.003-5.044				

4.770-4.802	5.078-5.172	4.932-5.014	5.040-5.075	4.947-5.009
4.851-4.879	4.959-4.990	4.978-5.037	5.019-5.037	5.034-5.087
4.929-4.965	5.002-5.036	5.022-5.054	4.989-5.028	4.953-5.024
5.008-5.030	4.965-5.009	4.970-5.014	4.972-5.049	4.963-4.990
4.976-5.029				

4.706-4.809	5.038-5.113	4.915-4.960	5.025-5.072	4.950-5.013
4.895-4.945	4.930-4.972	5.013-5.059	4.961-4.996	5.030-5.073
4.968-5.010	4.991-5.031	5.016-5.036	4.995-5.014	5.005-5.024
4.965-4.997	5.004-5.049	4.980-5.013	4.987-5.013	4.938-4.986
5.008-5.034				

4.789-4.945	5.056-5.136	4.932-5.037	4.897-5.041	4.990-5.063
4.886-4.965	4.951-5.006	5.042-5.082	5.015-5.065	5.011-5.032
4.983-5.027	4.988-5.018	4.979-5.039	5.004-5.042	5.043-5.088
4.980-5.061	5.033-5.082	4.979-5.029	4.997-5.026	4.985-5.003
5.001-5.060				

4.822-4.917	5.006-5.165	4.941-5.031	5.012-5.088	4.992-4.993
4.861-4.854	4.925-5.053	5.010-5.059	4.992-4.974	4.988-5.041
4.980-5.038	4.951-5.026	5.049-5.101	4.945-5.033	4.964-5.037
4.998-5.016	4.945-4.934	4.969-5.032	4.990-5.043	4.962-4.950
5.013-5.058				

5.062	5.033	5.078	5.053	4.914	4.930	5.112	4.891	4.951	4.997
4.940	4.957	5.002	5.031	5.006	4.989	4.991	5.027	4.954	5.055
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4.979-5.025 4.934-4.993 4.880-4.905 5.017-5.040 5.075-5.164
5.105-5.131 4.965-5.007 4.961-4.984 4.920-4.924 4.933-5.094
5.000-5.026 5.022-5.044 5.018-5.030 4.977-5.064 4.969-5.077
4.991-5.043 4.956-5.022 5.001-5.049 4.932-4.963 4.964-5.061
4.914-4.929

4.987 4.976 4.858 4.964 5.025 5.081 5.047 4.864 4.955 5.110
5.032 4.974 4.985 5.067 5.122 5.123 5.024 5.013 4.981 5.050
4.988

5.001 4.998 4.815 5.012 5.103 5.060 4.954 4.943 4.944 4.992
5.052 5.041 5.016 5.008 5.092 5.050 5.009 5.023 5.016 5.027
4.989

5.038 4.913 4.848 4.988 5.035 5.114 5.049 4.869 4.919 5.034
5.048 5.028 4.973 5.003 5.150 4.998 5.033 4.985 4.983 5.037
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4.916-4.956 4.928-5.010 4.961-5.049 5.182-5.265 4.918-5.066
4.985-5.019 4.966-5.095 4.973-4.993 4.981-5.004 5.011-5.070
4.992-5.046 4.999-5.040 5.015-5.057 5.012-5.036 4.976-5.000
4.997-5.013 4.993-5.005 4.955-4.992 4.981-5.011 4.989-5.003
4.979-5.004

4.941-5.001	4.908-5.037	5.010-5.152	4.982-5.065	4.955-5.069
5.017-5.034	5.033-5.061	4.967-5.003	5.002-5.022	5.027-5.053
5.037-5.072	4.942-4.967	4.975-5.027	4.995-5.003	5.000-5.013
5.012-5.023	4.975-5.004	4.971-5.006	4.980-4.997	4.988-5.004
5.011-5.027				

4.949-5.144	4.900-5.091	5.095-5.223	4.955-5.074	4.958-5.035
4.942-4.992	4.922-5.056	5.005-5.046	4.976-5.042	4.967-5.008
5.035-5.068	4.967-5.035	4.964-4.995	4.967-5.008	5.005-5.029
4.988-5.016	4.966-5.024	4.998-5.030	4.985-5.006	4.990-5.022
4.997-5.015				

5.054-5.060	4.981-5.089	5.082-5.170	4.916-4.969	4.937-4.983
4.992-5.056	4.977-5.023	4.946-4.981	5.011-5.032	4.988-5.007
5.031-5.066	4.917-4.952	4.970-5.070	4.977-4.986	5.004-5.032
4.978-5.003	4.989-5.020	4.994-5.042	4.984-5.002	4.987-5.022
5.001-5.028				

5.038-5.218	4.952-5.065	5.000-5.032	4.882-4.997	4.933-5.013
4.961-5.052	4.988-5.063	5.004-5.036	5.053-5.096	5.005-5.060
5.012-5.047	4.942-5.002	4.975-5.026	4.991-5.012	4.967-4.995
4.994-5.004	4.969-4.980	4.993-5.010	5.012-5.026	5.000-5.012
4.998-5.013				

5.029-5.209	4.983-5.066	4.964-5.092	4.839-4.911	4.976-4.989
4.976-5.086	5.009-5.038	4.971-5.073	4.986-5.046	5.034-5.064
5.016-5.041	4.967-4.986	5.010-5.046	4.980-4.997	4.996-5.061
4.958-4.991	5.014-5.023	4.973-4.995	4.996-5.013	4.980-5.006
5.006-5.020				

5.035-5.139	5.052-5.109	4.906-5.037	4.856-4.902	4.970-4.994
4.971-5.059	4.922-5.022	4.976-5.072	5.003-5.020	5.005-5.050
5.014-5.070	4.946-4.989	4.957-5.001	5.000-5.019	4.994-5.007
4.997-5.007	4.987-4.993	4.979-5.022	5.003-5.023	5.003-5.013
5.009-5.028				

5.007-5.058	5.122-5.142	4.884-4.998	4.899-4.947	5.002-5.019
4.909-4.949	4.913-5.000	5.018-5.034	4.978-4.995	4.997-5.056
5.082-5.092	4.995-5.022	4.995-5.037	4.967-5.033	4.994-4.997
5.013-5.080	4.928-5.024	4.972-5.027	4.997-5.030	4.974-5.034
4.962-5.026				

4.960-5.222	5.070-5.095	4.872-4.960	4.911-4.981	4.967-5.065
4.926-4.980	4.931-5.032	5.034-5.088	4.963-5.002	5.036-5.050

5.015-5.041 4.958-5.006 5.042-5.063 4.906-5.006 4.989-5.006
5.028-5.064 4.999-5.031 4.964-5.005 5.012-5.082 4.973-5.033
4.962-5.020

5.044-5.246 5.083-5.155 4.863-4.999 4.962-4.970 4.985-5.074
4.895-5.035 4.971-5.031 4.989-5.035 4.945-5.015 5.031-5.047
5.060-5.105 4.966-4.993 4.997-5.057 4.975-5.002 4.957-5.055
5.000-5.013 5.009-5.040 4.983-5.011 4.957-5.015 4.969-4.999
5.012-5.018

5.136-5.193 5.081-5.136 4.823-4.916 4.966-4.981 4.957-5.013
4.941-5.012 4.997-5.064 5.024-5.066 4.981-5.024 4.974-4.994
5.006-5.027 4.959-5.005 5.045-5.061 4.996-5.029 4.984-5.025
4.965-5.012 4.970-4.994 4.956-5.034 4.992-5.040 4.990-5.023
4.989-5.013

4.977-5.163 5.126-5.128 4.831-4.840 4.936-4.944 4.989-5.069
4.990-4.995 4.983-5.022 4.985-5.080 5.000-5.030 4.991-5.034
5.035-5.041 4.965-5.015 5.011-5.041 4.973-4.994 4.922-4.947
4.938-4.982 4.956-5.016 4.910-4.919 4.977-5.042 4.975-5.028
5.019-5.024

5.039 5.127 4.837 4.925 4.985 4.946 5.043 5.026 5.028 5.012
5.094 5.025 5.000 5.056 4.970 4.985 4.970 4.980 5.025 4.972
4.980

5.009 5.128 4.805 4.909 4.972 4.984 5.002 4.982 5.034 5.024
5.091 5.029 4.997 5.054 4.935 4.975 4.961 4.977 5.036 5.019
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4.960-4.969 4.864-4.917 5.040-5.060 5.122-5.248 4.803-4.933
5.076-5.124 4.908-4.915 4.983-5.008 4.961-4.997 4.907-4.946
4.890-5.023 4.954-5.038 4.978-4.983 4.983-4.998 4.985-5.020
5.004-5.012 5.015-5.030 4.993-5.021 4.994-5.048 4.999-4.999
4.991-5.007

4.960-4.993 5.082-5.086 5.032-5.128 5.155-5.180 5.013-5.071

5.051-5.058	5.040-5.111	4.932-4.937	5.003-5.015	5.005-5.048
4.999-5.074	4.978-4.981	4.965-5.018	5.018-5.040	4.994-5.002
4.977-5.001	5.005-5.028	4.906-4.957	4.988-5.002	4.990-5.034
4.997-5.001				

5.135-5.191	4.861-5.030	5.021-5.090	4.996-5.116	4.906-4.990
4.988-5.028	4.970-5.023	4.942-4.975	4.983-5.025	4.945-5.007
5.006-5.012	4.982-5.004	4.959-5.013	4.995-5.026	4.972-5.003
4.956-5.010	5.022-5.038	4.954-5.000	4.990-4.994	5.004-5.022
4.998-5.034				

5.135-5.202	4.944-4.971	4.970-4.996	4.991-5.045	4.943-4.977
4.991-5.026	5.020-5.056	4.886-4.958	4.990-5.021	5.019-5.045
4.971-5.042	4.932-4.955	4.981-5.004	5.004-5.030	4.994-5.017
4.986-5.008	4.997-5.003	4.996-5.003	4.984-5.002	4.967-5.004
4.990-5.012				

5.101-5.112	4.903-4.982	4.987-5.018	5.019-5.055	4.986-5.020
4.966-4.984	5.014-5.041	4.910-4.943	4.965-4.999	5.010-5.028
5.008-5.037	4.937-4.977	4.983-5.000	4.969-4.984	4.986-5.003
5.006-5.034	4.987-4.997	4.972-5.010	4.992-5.008	4.967-5.007
4.999-5.020				

5.099-5.144	4.849-4.933	4.964-4.993	5.051-5.087	5.006-5.037
4.953-4.973	5.015-5.055	4.945-4.978	4.959-5.003	5.026-5.072
4.962-5.023	4.949-4.985	4.975-5.009	4.951-4.980	4.984-5.034
4.976-5.011	5.001-5.022	4.988-5.019	5.000-5.007	4.975-5.012
4.987-5.005				

5.057-5.057	4.857-4.857	4.985-4.985	5.018-5.018	5.017-5.017
4.958-4.958	5.017-5.017	4.921-4.921	4.968-4.968	4.997-4.997
5.001-5.001	4.923-4.923	4.967-4.967	4.960-4.960	4.997-4.997
4.993-4.993	4.981-4.981	4.971-4.971	4.998-4.998	4.997-4.997
4.993-4.993				

5.045-5.070	4.853-4.888	4.966-5.015	5.023-5.056	5.028-5.065
4.957-4.981	5.006-5.023	4.943-4.984	4.982-5.015	4.968-5.020
4.983-5.019	4.940-4.993	4.975-5.005	4.966-4.984	5.008-5.048
4.997-5.035	4.987-5.018	4.978-5.005	5.012-5.034	4.985-4.996
4.975-5.017				

5.037-5.060	4.892-4.897	4.952-4.973	4.992-5.061	5.061-5.077
4.981-4.990	4.979-4.979	4.959-4.982	4.990-4.998	4.993-5.014
4.946-5.046	4.951-4.985	5.010-5.010	4.949-5.040	4.971-5.024
4.977-4.982	4.937-4.958	4.998-5.016	5.023-5.055	4.960-5.001

5.023-5.029

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5.085 5.039 5.016 4.995 5.034 4.985 4.976 5.019 5.042 4.969
4.975

5.061-5.082 4.771-4.816 5.020-5.035 4.873-5.030 4.809-4.926
5.041-5.142 4.939-4.980 5.001-5.044 4.974-5.058 4.939-4.994
4.911-5.033 4.922-5.069 5.006-5.011 4.988-5.014 4.992-4.998
4.982-4.984 4.975-5.032 5.008-5.023 4.990-5.010 4.972-5.001
4.982-4.990

4.982-5.245 4.744-4.950 4.957-5.020 4.961-5.041 4.992-5.168
4.842-5.097 5.053-5.171 4.829-5.090 5.034-5.036 4.978-5.026
4.982-5.050 4.972-5.044 4.991-5.012 4.956-5.025 5.008-5.040
4.975-4.998 4.991-5.025 4.971-5.039 4.985-5.005 5.011-5.018
4.981-4.989

5.010-5.044 4.762-4.793 4.779-5.032 4.992-5.173 4.899-5.002
5.022-5.101 4.979-4.997 4.931-5.009 5.030-5.040 4.994-5.033
4.966-5.007 5.029-5.034 5.041-5.073 4.964-5.039 4.913-5.055
4.961-5.013 4.952-5.013 4.933-5.009 4.980-5.049 4.979-4.991

4.938-5.015

4.980-5.222	4.783-4.807	4.949-5.028	4.952-4.963	5.036-5.093
4.945-4.971	4.986-5.042	5.018-5.115	4.986-5.110	5.072-5.102
5.025-5.058	5.015-5.099	5.029-5.066	4.998-5.035	5.034-5.060
4.925-4.951	5.022-5.068	5.065-5.072	4.986-4.998	4.969-5.018
4.985-5.034				

4.939-4.999	4.877-4.897	4.920-4.956	4.984-5.087	5.033-5.328
4.948-4.972	5.020-5.217	4.964-5.016	4.900-5.012	4.917-5.024
5.030-5.044	4.934-4.979	4.969-5.021	5.000-5.060	4.938-4.976
4.916-5.020	4.965-4.999	4.990-5.002	4.998-5.019	4.993-5.016
4.977-5.033				

4.897-5.035	4.848-4.907	4.768-4.938	5.019-5.056	5.034-5.044
4.973-5.051	4.934-4.983	4.960-4.988	4.965-5.023	4.993-5.066
4.978-4.980	4.900-4.918	4.891-5.025	4.964-5.017	5.014-5.020
4.942-4.975	4.977-5.087	5.006-5.009	4.956-5.007	5.030-5.100
5.002-5.035				

5.078-5.082	4.788-4.856	4.952-4.990	4.952-4.973	5.005-5.051
4.942-5.014	5.028-5.083	4.984-5.025	4.865-5.018	5.007-5.021
4.943-5.038	4.959-5.033	5.004-5.029	4.968-5.013	4.868-5.031
4.980-5.076	4.957-4.969	5.014-5.052	5.036-5.055	4.978-4.994
4.955-4.986				

5.005-5.102	4.746-4.831	4.930-5.058	4.959-4.974	5.033-5.084
4.891-4.899	4.987-5.089	4.905-5.121	4.862-4.957	5.012-5.051
4.935-4.981	5.006-5.027	4.945-4.996	4.999-5.067	4.931-5.016
4.920-4.938	4.990-5.054	4.960-5.044	4.983-4.996	4.972-5.053
4.981-5.014				

5.012-5.084	4.773-4.814	4.943-5.014	4.894-4.918	4.995-5.089
4.828-5.007	4.993-5.049	4.918-5.053	4.919-5.069	5.005-5.029
4.980-5.011	4.979-4.999	4.959-5.032	4.979-5.025	4.901-4.987
4.874-4.971	5.004-5.030	5.023-5.054	4.993-5.004	4.897-5.004
4.951-4.986				

5.060-5.068	4.760-4.813	4.993-5.002	4.983-5.009	4.933-5.063
4.885-4.973	5.055-5.063	4.990-5.044	4.998-5.057	4.916-5.059
5.027-5.038	4.933-4.971	4.900-4.980	5.073-5.074	4.969-5.001
5.009-5.031	4.937-4.944	4.989-4.991	4.944-5.019	5.012-5.020
4.981-5.037				

4.971	4.863	4.904	4.921	5.034	5.016	5.057	4.993	4.966	5.055

4.966 5.014 4.959 5.023 5.057 4.945 5.010 5.031 4.976 4.969
4.958

4.987 4.849 4.959 4.988 5.024 5.005 5.051 4.995 4.928 5.003
5.047 5.045 4.987 4.938 4.978 5.000 5.030 5.049 4.965 5.026
5.046

4.989 4.907 4.920 4.975 5.001 5.047 5.075 5.081 4.952 5.061
5.004 5.043 4.936 4.941 4.979 5.018 5.070 5.020 4.937 5.047
5.034

4.965 4.937 5.000 5.001 5.056 5.019 5.036 5.007 4.988 5.016
5.022 5.018 5.039 4.973 5.000 5.051 4.990 5.001 4.996 5.023
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4.970 4.933 5.068 5.145 4.974 5.048 4.966 4.936 5.072 4.897
4.934 5.075 4.959 5.030 5.031 5.017 4.944 4.989 4.974 4.984
5.042

4.965-5.052 4.689-4.919 4.903-5.141 4.800-5.025 4.834-4.999
4.973-5.107 4.866-5.056 4.879-4.952 4.969-5.008 4.898-4.984
4.937-5.104 4.971-5.065 4.951-4.988 4.989-5.004 4.978-5.022
4.962-5.005 4.982-4.996 4.998-4.998 4.998-5.019 4.971-5.045
4.955-5.017

4.984-5.040 4.756-4.970 4.941-5.032 4.958-5.002 4.920-5.103
5.000-5.081 4.906-5.075 4.905-5.079 4.981-4.998 4.939-4.958
4.957-5.009 5.012-5.084 4.981-4.998 4.967-5.009 4.980-5.020
4.980-5.025 5.028-5.033 4.985-5.014 4.976-4.994 4.960-4.977
4.991-5.022

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5.157-5.060 4.920-4.723 5.004-5.000 5.057-5.046 5.061-4.968
4.977-4.904 5.000-4.888 5.005-5.004 5.016-4.992 4.921-4.908
5.064-4.848 5.039-4.995 5.077-5.002 5.032-5.014 5.020-4.985
5.027-4.973 5.030-5.005 5.018-4.981 5.019-4.993 5.012-4.982
5.034-4.998

4.975-5.081 4.757-4.908 4.967-5.039 4.955-5.024 4.946-5.067
4.982-5.013 4.923-4.933 5.020-5.032 4.999-5.025 4.937-4.973
4.920-5.019 4.974-5.051 4.975-5.018 4.986-5.031 5.022-5.030
4.950-5.038 4.985-5.001 4.961-5.032 4.995-5.046 4.958-4.990
4.999-5.019

5.091-5.123 4.747-4.846 5.002-5.018 4.905-4.957 4.986-5.059
4.986-5.021 4.910-4.930 5.017-5.062 4.992-5.017 4.961-4.982
4.957-5.001 4.984-5.014 4.954-4.997 4.970-4.988 4.973-5.030
5.020-5.048 4.986-5.013 5.017-5.044 4.967-5.004 4.981-5.021
4.956-5.008

5.036-5.145 4.708-4.735 4.985-5.063 4.929-5.022 4.946-4.948
4.907-5.009 4.947-4.979 5.017-5.078 4.982-5.032 4.947-5.037
4.949-4.971 5.009-5.065 5.010-5.017 4.973-4.980 4.980-5.059
4.975-4.967 4.945-4.970 4.984-5.032 4.972-4.980 4.965-4.993
5.003-5.046

4.984-5.103 4.688-4.733 4.977-5.047 5.016-5.045 4.969-4.987
4.901-4.970 4.966-4.981 5.041-5.054 5.023-5.026 4.967-4.993
4.953-4.978 5.020-5.076 4.974-5.000 4.956-4.989 5.027-5.045
4.994-5.054 5.016-5.025 4.995-5.012 4.980-4.991 4.986-4.993
4.959-4.988

5.094-5.142 4.711-4.770 4.956-5.007 5.047-5.107 4.921-5.013
4.914-4.935 4.921-4.988 5.012-5.041 4.995-5.021 4.930-4.965
5.003-5.030 5.012-5.048 4.962-5.005 5.002-5.042 5.002-5.015
4.989-5.041 4.966-4.974 4.966-4.984 4.985-5.024 5.005-5.016
5.007-5.021

5.042-5.077 4.695-4.748 4.972-4.980 5.043-5.077 4.897-4.959
4.917-4.970 4.956-5.020 5.043-5.056 4.984-5.023 4.939-4.962
5.000-5.024 5.005-5.041 4.979-5.028 4.993-5.035 4.965-5.042
4.996-5.011 4.977-5.010 4.978-5.005 4.981-5.016 4.987-5.028
4.976-4.994

5.072 4.720 4.998 5.116 4.913 4.923 5.027 5.081 4.955 4.919
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4.982 5.184 5.149 5.183 4.997 5.044 5.030 4.983 5.004 5.051
5.052 4.979 5.010 5.024 4.965 5.015 4.980 4.975 4.995 5.016
5.029

5.132 4.864 5.168 4.876 4.899 5.018 4.907 5.045 5.001 4.987
5.051 5.008 4.977 4.997 5.004 5.000 5.001 5.005 4.986 4.996
5.017

5.045-5.120 4.788-4.986 4.941-5.007 4.898-4.988 4.938-5.063
5.006-5.054 4.908-5.002 4.962-5.059 4.926-5.047 4.977-5.056
4.981-5.014 5.021-5.060 4.977-5.000 4.962-4.999 4.986-5.008
4.993-5.046 4.972-5.010 4.979-5.037 4.987-5.005 4.970-4.979
4.973-5.009

5.133 5.015 4.997 4.957 5.110 5.014 4.879 4.919 4.940 5.049
5.019 5.019 5.002 4.973 4.951 4.975 4.993 5.028 4.962 4.995
4.996

5.052 5.096 5.050 4.890 5.069 4.932 5.009 4.962 4.944 4.955
4.956 4.878 5.012 5.051 5.026 4.961 4.982 5.023 4.950 4.933
5.033

5.002 5.079 5.085 4.912 5.025 5.052 5.083 4.849 5.062 4.902
5.188 4.983 4.981 5.106 5.019 5.013 4.994 5.028 4.959 5.030
4.946

5.054 4.936 4.977 4.882 5.053 5.067 4.784 4.991 4.901 5.045
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4.974-4.992	4.899-5.179	4.948-5.031	4.869-5.117	4.921-4.931
4.998-5.152	4.964-4.994	4.958-4.967	4.988-5.078	4.942-4.993
4.986-5.006	4.979-4.980	4.929-5.026	4.997-5.015	5.007-5.023
5.009-5.022	4.951-4.991	4.989-4.996	4.967-4.999	4.986-4.988
4.976-5.010				
4.901-5.042	4.838-5.096	5.079-5.133	4.911-4.990	4.934-4.955
5.040-5.120	4.885-4.970	4.941-5.118	4.923-5.048	4.963-5.044
4.982-5.016	4.911-5.037	4.967-5.055	4.905-5.064	4.973-5.001
4.992-5.005	4.975-4.996	4.986-5.002	5.003-5.045	4.974-4.997
4.988-4.995				
4.996-5.112	4.913-5.073	4.980-5.119	4.879-4.993	4.954-4.961
5.086-5.119	4.846-4.944	4.879-4.958	4.944-4.979	5.019-5.025
5.035-5.040	4.932-5.136	4.974-5.018	4.935-4.978	4.938-5.042
4.993-5.016	4.991-5.030	4.927-4.968	4.972-4.991	4.976-4.999
4.973-5.024				
5.124-5.137	4.795-4.925	4.954-5.061	4.976-5.013	5.039-5.059

4.993-5.045 4.871-4.887 4.999-5.072 4.995-5.085 4.982-5.034
4.978-5.042 5.022-5.036 4.936-5.051 4.931-4.974 4.982-5.063
4.942-5.043 4.963-5.060 5.013-5.014 4.961-5.034 4.973-5.007
4.985-5.005

4.921-5.118 4.808-4.971 5.015-5.031 4.959-5.021 5.034-5.112
5.007-5.081 4.904-5.032 4.999-5.079 4.976-4.992 4.999-5.024
4.915-4.984 4.944-5.029 4.981-4.996 4.943-5.029 4.954-5.017
4.973-4.987 4.987-5.118 4.961-5.010 5.004-5.097 4.993-5.025
5.005-5.010

5.015-5.123 4.726-4.870 4.976-5.066 4.987-5.023 5.007-5.080
5.013-5.015 4.876-5.016 5.039-5.065 5.035-5.100 4.977-5.015
5.005-5.059 4.957-4.964 4.990-5.006 4.948-4.959 4.933-4.985
4.961-5.033 5.055-5.074 4.963-5.048 4.997-5.034 5.006-5.008
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APPENDIX 5

Zeacolpus TNT matrix. Pages 267-302 contain the character data. Pages 303-314 contain weighting code for the various analyses presented in chapter 2. To run a weighted analysis, one of the Ccode blocks should be appended to the end of the character code after the last semicolon.

nstates cont;
xread
'Chapter 2: Zeacolpus: 21 eigenaxes'
430 19
&[cont]

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4.966-5.029

4.928-4.972 4.777-4.975 4.800-4.822 4.963-5.014 4.939-5.008
4.965-4.999 4.976-5.044 4.939-4.984 4.976-5.027 4.948-4.964
4.927-5.007 4.896-4.997 4.974-5.023 4.988-5.067 5.001-5.058
4.963-5.051 4.988-5.005 4.974-5.019 5.019-5.034 4.953-5.019
4.992-5.057

4.920-4.949 4.856-5.046 4.935-5.038 4.932-5.069 4.935-4.976
4.978-5.059 4.996-5.068 5.018-5.039 4.977-5.026 4.916-4.967
4.954-4.998 4.949-5.017 4.991-5.028 4.979-4.986 4.990-5.008
5.002-5.031 4.999-5.014 4.977-4.995 4.965-5.011 5.030-5.044
4.977-5.021

4.874-4.896 4.842-4.926 4.964-5.076 4.937-4.967 4.908-4.967
5.013-5.093 5.003-5.072 5.015-5.038 5.006-5.040 4.936-5.007
4.965-4.986 5.018-5.058 5.021-5.057 4.964-4.991 4.960-4.989
4.992-5.051 4.974-5.004 4.985-5.006 4.992-4.998 4.983-5.030

4.991-5.021

4.840-4.900	4.829-4.924	4.972-5.045	4.938-4.989	4.949-4.997
5.013-5.022	4.999-5.050	4.979-5.033	4.982-5.038	5.001-5.035
5.003-5.037	5.038-5.084	5.004-5.033	4.947-4.964	4.979-4.998
4.994-5.027	4.984-5.009	4.976-5.026	5.005-5.022	4.974-5.016
5.002-5.025				

4.916-4.935	4.855-4.958	4.968-5.031	4.972-5.020	4.899-4.966
5.045-5.069	5.004-5.052	4.974-4.977	4.997-5.003	4.961-4.995
4.999-5.011	5.005-5.045	4.959-4.989	4.967-4.988	4.998-5.038
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4.997-5.005				

4.891-4.906	4.832-4.883	4.948-5.020	4.961-4.988	4.933-4.966
5.074-5.079	4.995-5.034	4.917-4.965	4.999-5.019	4.991-5.016
5.001-5.027	4.993-5.013	4.954-4.968	4.971-5.002	4.982-5.002
5.021-5.049	4.987-5.000	4.955-4.981	5.004-5.024	4.980-5.019
4.977-5.002				

4.904-4.918	4.902-5.036	4.931-5.050	4.974-5.017	4.952-4.979
5.029-5.075	4.950-4.988	4.963-5.022	5.014-5.047	5.007-5.054
5.013-5.033	5.023-5.039	4.982-5.016	4.968-4.984	4.983-5.007
4.985-5.029	4.981-5.011	4.986-5.014	4.972-5.009	4.976-5.018
4.965-4.989				

4.912-4.925	4.845-5.004	4.982-5.016	4.996-5.057	4.931-5.040
5.057-5.107	4.907-4.984	4.982-4.997	4.988-5.022	5.007-5.042
5.007-5.020	4.976-5.037	4.989-5.006	4.958-5.011	4.979-5.033
5.009-5.027	5.026-5.046	5.018-5.040	4.994-5.026	4.967-5.056
4.960-4.975				

4.940-4.966	4.840-4.952	4.949-4.990	5.047-5.050	4.956-5.015
5.090-5.097	4.935-5.031	4.956-5.001	4.999-5.047	4.988-5.060
4.986-5.076	4.983-5.045	4.983-5.001	5.020-5.029	5.014-5.025
5.009-5.059	4.944-4.949	4.976-4.977	4.993-5.037	5.007-5.026
4.981-4.999				

5.066	4.921	4.885	5.162	4.983	5.151	4.970	4.998	5.014	4.983
4.977	5.053	4.940	5.050	5.056	4.962	4.952	5.007	5.033	5.022
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5.129-5.192	4.899-4.927	4.882-4.947	4.995-5.050	5.005-5.048
5.049-5.095	4.954-5.042	4.956-4.987	5.011-5.040	4.975-5.018
4.983-5.022	4.952-5.012	4.955-5.019	4.996-5.067	4.991-5.002
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4.967-4.989				
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4.965-5.010	4.985-5.029	4.958-4.988	4.999-5.029	4.992-5.026
4.999-5.042	4.955-4.993	4.977-5.008	4.985-5.005	4.996-5.020
4.974-5.023	4.986-5.017	4.988-5.009	4.973-4.995	4.982-4.995
4.983-5.000				
5.109-5.137	5.065-5.121	4.970-5.038	4.980-5.018	4.946-4.974
4.972-5.004	4.950-4.999	4.975-5.012	5.008-5.042	4.996-5.012
4.972-5.006	4.994-5.008	4.988-5.017	4.982-5.001	4.968-5.009
5.023-5.041	4.992-5.011	4.994-5.009	4.991-5.004	4.997-5.009
4.997-5.021				
5.035-5.078	5.039-5.094	5.046-5.121	4.943-4.977	4.950-4.969
4.989-5.014	4.965-4.990	4.971-5.016	5.000-5.030	4.954-4.988
5.001-5.030	5.012-5.032	4.962-4.983	4.972-5.001	5.012-5.033
5.018-5.030	4.980-5.005	4.976-5.003	4.981-4.997	4.990-5.006
4.962-4.984				
4.986-5.021	5.025-5.086	5.040-5.128	4.959-4.991	4.971-4.999
4.953-4.992	4.993-5.016	4.972-5.004	4.990-5.023	4.983-5.018
4.986-5.019	4.997-5.028	4.964-4.998	4.993-5.013	4.966-5.005
5.004-5.026	4.973-4.996	5.010-5.035	4.996-5.012	4.994-5.008
4.986-5.004				
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4.967-5.000				

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4.984-5.011	4.994-5.014	4.990-5.006	4.992-5.016	4.977-4.993
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4.998-5.020	4.966-4.997	5.001-5.030	4.992-5.037	4.981-4.996
4.987-5.015	4.988-5.015	4.981-5.014	5.010-5.036	4.943-4.984
4.993-5.015				

4.874-4.916	4.913-5.043	5.029-5.110	4.954-4.991	4.994-5.048
4.999-5.051	4.996-5.032	5.004-5.048	5.042-5.069	4.956-4.988
5.009-5.048	5.000-5.017	5.007-5.058	5.005-5.034	4.990-5.023
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5.004-5.021				

4.862-4.902	5.033-5.068	5.031-5.113	4.929-4.951	5.041-5.067
5.016-5.059	4.973-4.992	4.964-5.026	4.985-5.050	4.975-5.003
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4.981-5.023	4.957-5.016	4.966-4.996	4.974-5.011	4.964-5.010
4.993-5.032				

4.836-4.902	4.987-5.058	5.015-5.072	4.915-4.955	5.063-5.091
5.009-5.073	4.966-4.985	4.959-5.074	5.005-5.021	4.976-4.992
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4.985-5.027				

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4.992-5.025	4.979-5.001	4.927-4.992	4.985-5.081	4.992-5.049
4.972-4.988	4.978-5.001	4.943-5.046	4.986-5.026	4.968-5.015
4.987-5.034	4.937-5.014	4.973-5.016	4.964-5.006	5.001-5.044
4.966-5.021				

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5.035-5.090	4.949-4.964	4.944-5.025	5.031-5.087	4.982-4.999
4.981-5.045	4.976-4.982	5.047-5.049	5.029-5.057	4.942-5.030
5.021-5.068	4.901-5.117	5.011-5.070	4.899-5.022	5.016-5.079

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5.212 4.895 5.088 4.943 4.901 4.891 4.859 4.985 4.978 4.982
4.954 4.947 4.948 5.035 4.970 4.972 5.043 4.978 5.016 5.032
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5.115 4.762 5.206 4.931 5.000 4.846 4.799 4.952 4.984 4.992
4.964 5.022 5.032 5.004 5.015 4.952 5.052 4.986 5.014 5.030

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4.995 5.030 4.837 4.898 4.974 4.880 5.080 4.988 4.913 4.991
5.029 5.065 5.086 5.078 5.003 4.994 5.041 4.946 5.018 5.025
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4.991-5.072 4.914-5.042 4.983-5.210 4.966-5.002 4.901-4.999
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4.985-5.058 4.890-5.109 4.911-5.142 5.011-5.058 4.807-4.948
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4.952-4.992 4.961-5.026 5.022-5.031 4.995-5.000 5.010-5.024
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4.953-5.025 4.965-5.169 4.855-5.179 4.990-5.025 4.923-4.996
4.932-5.000 5.010-5.026 4.962-5.000 4.983-5.014 4.891-4.992
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4.950-5.012 4.942-5.117 5.090-5.259 4.959-5.029 4.965-5.031
4.939-5.002 5.025-5.057 4.923-5.014 4.917-4.999 5.007-5.031
4.901-4.964 4.990-5.029 5.032-5.064 4.974-5.056 4.949-5.032
4.996-5.010 4.979-5.023 4.995-5.047 4.990-4.996 4.995-5.039
4.925-4.982

4.932-5.009 5.073-5.247 4.989-5.054 4.976-5.169 4.812-4.998
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4.991-5.004 5.009-5.055 5.058-5.144 4.995-5.034 4.886-4.985
4.948-5.004 4.973-4.985 4.921-5.070 4.941-5.078 4.964-5.029
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4.934-4.954 5.108-5.207 4.974-5.089 4.925-5.044 4.955-5.120
4.920-5.029 4.981-5.078 4.895-5.164 4.891-5.066 4.950-4.968
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4.980-5.041 4.988-4.995 4.943-4.984 4.958-5.084 5.001-5.006
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4.963 5.076 4.904 5.078 4.968 4.989 4.968 5.007 4.950 4.948
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4.928 5.048 4.960 5.043 5.013 4.977 4.977 5.020 4.987 5.001
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4.870 5.015 4.915 5.056 4.983 4.989 4.962 4.981 4.999 5.013
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5.129 5.122 5.137 5.130 4.971 4.953 4.977 4.984 5.078 5.021
4.955 5.017 4.901 4.998 4.926 4.981 4.937 5.057 5.031 5.052
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5.092 5.129 5.161 5.165 4.915 5.106 5.009 4.938 5.031 4.966
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5.029 5.006 5.016 5.068 4.994 5.054 4.944 4.996 5.105 4.960
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5.127-5.219 4.762-4.990 4.939-5.001 4.943-5.102 4.945-5.141
4.942-4.965 4.890-5.009 5.021-5.091 4.925-5.020 5.063-5.076
4.999-5.061 4.921-4.991 4.949-5.005 5.045-5.048 5.005-5.106
4.983-4.983 4.967-5.066 4.948-5.016 4.997-5.002 4.992-5.029
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4.917-5.011 4.979-5.064 4.913-4.991 5.041-5.044 4.984-5.031
5.010-5.026 4.936-5.047 4.998-5.061 4.985-5.030 5.052-5.131
4.948-5.013 4.970-5.023 4.975-5.014 5.019-5.067 4.979-5.020
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5.009-5.073 4.875-4.970 5.099-5.132 5.089-5.111 4.995-5.038
4.966-5.010 5.004-5.088 4.986-5.032 4.995-5.017 4.980-5.002
4.942-5.010 4.991-5.000 4.967-5.035 5.026-5.054 5.002-5.095
5.016-5.069 4.989-5.019 5.000-5.017 4.978-4.980 4.976-5.000
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5.013-5.043 4.971-5.094 5.058-5.109 5.071-5.098 4.984-5.050
5.017-5.051 5.012-5.086 4.988-5.034 4.975-4.993 4.935-4.966
4.974-5.058 4.973-4.987 4.994-5.018 4.976-4.984 4.971-5.024
5.016-5.054 4.979-5.024 4.988-4.993 4.962-5.001 4.972-5.012
5.017-5.047

4.990-5.005 4.892-5.048 5.042-5.141 5.043-5.085 5.002-5.008
5.020-5.050 4.998-5.107 4.945-4.972 4.982-5.017 4.958-4.973
4.949-5.008 4.994-5.016 4.956-4.985 4.999-5.011 4.994-5.022
5.010-5.014 4.986-5.039 4.972-4.983 5.011-5.026 4.995-5.005
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4.956-4.992 4.939-5.051 4.938-5.074 4.995-5.025 5.006-5.042
5.004-5.045 5.016-5.065 4.964-4.985 4.939-4.988 4.953-5.004
4.988-5.001 4.913-4.996 4.988-5.028 5.030-5.063 4.963-5.000
4.974-4.997 4.979-5.031 4.967-4.998 4.943-4.972 4.996-5.005
5.003-5.011

4.907-4.960 4.940-5.051 4.947-5.062 5.032-5.083 5.005-5.028
5.002-5.034 5.017-5.057 4.970-5.018 4.960-5.022 4.979-4.996
4.981-5.040 4.988-5.018 4.970-5.003 5.003-5.037 4.990-5.017
4.989-5.008 4.985-5.002 4.972-4.993 4.974-5.019 4.986-5.021
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4.893-4.910 5.003-5.069 4.963-5.024 5.050-5.090 4.992-5.045
4.965-5.034 4.998-5.010 4.973-4.989 4.968-5.011 4.979-5.026
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4.977-5.004 4.991-5.025 5.003-5.021 4.980-5.025 4.983-5.015
4.997-5.010

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4.952-5.012 4.984-5.018 5.033-5.059 4.996-5.024 5.004-5.008
4.987-5.053 4.987-4.988 4.988-4.993 4.987-4.989 5.005-5.020
4.976-5.008 4.985-5.008 4.974-4.990 4.962-5.045 4.939-4.997
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4.796-4.868 5.001-5.023 4.948-4.993 5.023-5.073 5.015-5.036
4.954-4.987 5.008-5.011 4.994-5.027 4.991-5.020 5.020-5.042
4.978-5.038 4.971-4.984 4.974-4.986 5.013-5.025 4.999-5.008
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4.886-4.952 4.960-5.070 4.881-4.995 4.936-5.080 4.962-5.049
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5.021-5.097 4.987-5.036 4.988-5.034 4.935-5.054 4.995-5.030
5.023-5.052 5.023-5.036 4.989-5.004 5.009-5.011 4.995-5.015
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4.925-5.021 4.891-5.002 4.944-5.127 4.912-4.984 4.926-5.017
5.007-5.084 5.013-5.041 5.006-5.088 4.974-5.065 4.981-4.992
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4.933-4.988 4.991-5.001 4.994-5.016 4.992-5.029 4.994-5.004
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4.905-5.017 4.898-5.144 4.809-5.109 4.979-4.992 4.983-5.048
4.974-5.030 5.026-5.088 5.089-5.115 4.966-5.115 4.988-5.016
4.999-5.096 4.985-5.021 5.010-5.067 4.930-5.068 4.969-5.011
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4.919-4.977 5.020-5.034 5.017-5.029 4.980-5.029 4.914-5.025
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5.055-5.103 5.026-5.050 4.935-4.981 4.911-4.966 4.963-5.007
5.015-5.036 4.953-4.998 4.908-4.969 4.993-5.015 4.982-5.014
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5.048-5.090 5.035-5.047 4.899-4.950 4.927-4.952 5.000-5.018
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4.989-5.007 5.010-5.034 5.016-5.045 4.984-5.004 5.007-5.035
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4.975-5.022 4.980-5.004 5.014-5.043 4.966-5.022 4.950-4.969
4.961-4.992 4.978-5.004 4.997-5.019 4.993-5.022 4.992-5.010
4.990-5.006

4.959 5.036 5.042 4.917 5.000 4.991 5.007 5.045 5.030 4.955
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4.896 5.111 4.900 5.100 5.022 4.932 4.996 5.034 4.977 4.936
5.044 4.999 5.038 4.993 4.934 4.998 5.055 4.986 5.031 4.951
5.000

4.863-4.915 5.059-5.066 4.925-5.003 4.972-5.075 5.026-5.030
4.964-5.023 4.986-5.044 5.039-5.044 4.989-5.009 4.968-5.074
4.986-5.046 4.977-5.001 4.999-5.029 4.955-5.012 4.994-5.006
4.956-5.022 4.943-4.992 4.971-5.006 4.986-4.993 4.915-5.036
4.947-4.952

4.866-4.906 5.036-5.041 4.921-4.979 5.082-5.104 5.003-5.032
4.949-5.031 4.972-5.034 4.978-5.036 4.965-4.976 5.025-5.037
4.937-5.070 4.956-4.960 4.957-5.008 4.961-5.018 4.998-5.016
4.968-5.002 4.994-5.009 5.020-5.028 5.021-5.034 4.949-4.997
4.991-5.031

4.800-4.827 5.003-5.036 4.941-4.968 5.005-5.016 5.038-5.079
4.956-5.069 5.041-5.060 4.955-5.066 4.956-4.973 5.009-5.028
4.962-5.015 4.954-4.982 4.923-4.996 4.935-4.943 4.990-5.020
5.023-5.041 4.981-5.011 4.989-4.996 5.004-5.018 4.957-4.980
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4.850-4.887 4.994-5.000 4.960-5.031 5.009-5.021 4.991-5.064
5.031-5.060 5.020-5.028 4.999-5.044 4.972-5.012 5.036-5.081
5.022-5.049 4.898-4.948 4.886-4.971 4.903-4.983 4.986-5.027
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5.035 5.143 5.058 5.074 5.020 5.011 4.991 5.055 4.941 5.134

4.973 4.981 5.037 4.982 4.974 4.997 4.999 4.987 5.008 4.990
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4.989 5.142 4.992 4.974 5.140 4.989 5.000 4.974 5.046 5.012
4.998 4.955 5.055 4.984 4.940 5.092 4.934 5.049 5.061 4.997
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4.956 5.055 5.119 5.069 5.077 5.053 5.013 4.966 4.942 5.043
5.052 5.052 5.020 5.014 5.038 4.998 4.993 5.037 4.985 4.964
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4.946 5.067 5.169 5.064 5.088 5.114 5.000 4.949 4.888 5.038
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4.854-4.909 4.961-5.071 5.013-5.105 4.982-5.044 5.038-5.199
5.068-5.084 4.956-4.981 4.979-5.015 4.950-4.972 4.924-4.964
4.959-4.987 4.978-4.998 4.970-4.987 5.022-5.042 4.996-5.034
5.000-5.043 5.007-5.035 4.993-5.001 5.000-5.010 4.975-5.021
5.003-5.037

4.876 4.933 5.057 5.116 4.972 5.084 4.977 4.908 5.055 5.030
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4.957 5.002 4.972 5.013 4.952 5.014 5.059 4.990 5.078 4.988
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4.929-5.040	4.953-4.962	5.014-5.056	4.906-5.068	4.958-5.038
4.971-4.975	4.995-5.161	5.036-5.041	4.954-5.031	4.941-5.018
5.043-5.052	4.957-4.981	4.995-5.014	4.979-4.983	4.986-5.025
5.024-5.041				

5.120-5.176	4.884-5.010	4.736-5.149	5.003-5.123	4.963-5.049
4.856-5.022	4.944-4.961	5.023-5.028	4.975-4.991	5.011-5.054
4.975-5.014	4.951-5.072	4.942-5.095	5.027-5.042	5.004-5.033
5.014-5.023	4.981-5.027	4.986-5.042	4.981-5.023	4.991-5.012
4.975-5.008				

5.026-5.083	4.648-4.710	4.964-5.080	4.932-4.985	5.090-5.150
4.901-4.982	4.989-5.037	5.014-5.035	4.953-4.988	4.973-5.034
4.980-5.059	4.965-5.033	5.001-5.021	4.994-5.030	5.059-5.075
5.010-5.020	4.967-5.032	4.891-4.940	4.966-5.016	4.969-4.994
4.990-4.994				

5.000-5.028	4.707-4.722	4.868-5.033	4.974-4.990	4.973-5.138
4.976-5.040	4.985-5.028	4.924-4.963	4.841-4.901	4.962-5.010
4.957-4.957	4.972-5.009	4.941-4.997	5.006-5.059	5.028-5.059
4.979-5.049	5.000-5.095	4.977-5.045	4.970-4.989	5.000-5.001
4.987-5.003				

4.992-5.012	4.787-4.789	4.990-5.045	4.984-5.023	4.982-5.028
4.973-5.019	5.028-5.068	5.035-5.057	4.936-5.011	4.983-5.048
4.998-5.005	4.864-4.977	4.978-4.991	4.960-5.032	4.995-5.012
4.943-4.987	4.956-4.987	4.994-5.014	4.956-5.002	5.007-5.020
4.992-5.012				

4.948-4.980	4.757-4.796	5.034-5.139	4.983-5.014	4.997-5.030

4.984-5.000 4.993-5.025 4.952-4.968 5.032-5.088 4.904-5.093
4.979-5.001 4.949-4.979 5.006-5.042 4.899-4.955 4.933-4.981
4.937-5.009 4.936-5.007 4.983-5.054 4.976-5.026 4.944-4.967
4.996-5.006

4.966-5.013 4.773-4.811 4.833-5.016 4.994-5.029 4.978-4.999
4.982-5.000 5.059-5.081 4.988-5.029 4.936-5.082 4.966-4.975
5.008-5.046 4.903-5.134 4.911-4.989 4.974-5.027 4.954-4.959
4.930-5.063 4.958-5.001 4.973-5.002 4.940-4.966 5.035-5.040
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5.205 5.139 5.002 5.146 4.943 5.028 4.944 5.015 4.990 4.967
4.981 4.970 5.059 5.021 4.996 4.986 4.987 5.004 4.960 4.994
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5.182 5.155 5.015 5.038 4.941 5.072 4.995 5.005 4.991 4.919
5.012 4.995 5.043 5.029 4.978 5.030 5.020 4.991 4.963 4.993
5.037

5.061 5.104 4.729 4.940 4.987 4.848 5.065 5.019 5.085 4.955
4.948 5.050 5.044 5.018 5.019 4.977 4.940 4.937 4.929 5.015
4.995

5.037-5.065 4.953-5.043 4.944-5.062 4.936-4.990 4.961-5.005
4.986-5.055 4.945-5.010 4.982-5.010 4.928-4.980 5.021-5.043
5.003-5.087 5.029-5.044 4.951-5.015 5.035-5.071 5.014-5.066
5.017-5.024 5.006-5.043 4.996-5.029 5.028-5.072 4.987-5.050
5.000-5.013

5.023-5.042 4.984-5.085 4.874-5.081 4.977-5.051 4.935-4.966
5.041-5.050 4.976-4.998 4.945-5.001 4.924-4.949 4.915-5.055
5.019-5.118 4.972-5.075 4.983-5.045 4.966-5.050 4.999-5.036
4.993-5.032 4.968-5.027 4.982-4.998 4.985-4.997 4.937-4.989
4.993-4.994

4.995-5.013 5.057-5.111 4.919-5.044 4.994-5.003 5.004-5.066
4.946-5.000 4.973-4.980 5.010-5.052 4.946-4.953 4.962-5.029
4.996-5.045 4.995-5.019 4.974-5.025 4.965-5.003 5.022-5.045
4.936-5.059 4.987-4.988 4.998-5.029 4.973-5.029 4.994-5.028
5.002-5.016

4.980-5.007	5.019-5.105	4.894-5.064	4.990-5.004	4.947-5.049
4.961-5.062	5.010-5.070	5.000-5.007	4.971-4.997	4.982-5.069
4.964-4.973	5.004-5.032	4.967-5.055	4.994-4.999	4.981-5.076
5.019-5.026	4.947-5.057	5.006-5.009	4.980-4.994	5.032-5.034
5.002-5.006				

4.971-4.983	5.075-5.151	4.901-5.037	4.920-5.024	4.915-5.007
4.964-4.964	4.962-4.995	5.017-5.108	4.972-5.076	4.976-4.987
4.996-5.008	5.011-5.038	4.929-4.994	4.965-4.985	4.969-5.026
4.917-4.962	4.975-5.056	4.989-5.004	4.991-5.041	4.967-5.022
4.993-5.008				

4.920-4.920	4.947-5.071	4.968-4.999	5.005-5.017	5.014-5.093
4.969-5.042	4.993-5.003	4.993-4.999	5.000-5.019	4.936-5.017
5.015-5.024	5.012-5.034	4.980-4.983	4.972-5.004	4.938-5.037
4.970-4.996	4.996-5.049	5.023-5.025	4.970-4.998	4.972-5.031
5.000-5.002				

4.849-4.904	4.989-5.044	4.901-4.998	5.050-5.090	4.976-5.014
4.980-5.007	4.979-4.992	4.994-5.031	4.956-5.018	4.976-5.031
4.990-5.019	5.001-5.051	5.000-5.042	4.983-5.039	4.988-5.052
4.990-5.000	4.957-5.016	4.981-5.021	4.988-5.010	4.970-5.036
4.984-4.993				

4.820-4.858	4.968-5.012	4.924-4.969	5.042-5.102	4.922-4.956
4.972-5.033	4.942-4.965	4.946-5.004	5.002-5.039	4.976-4.993
5.004-5.019	4.987-5.022	5.015-5.020	5.019-5.041	5.006-5.042
4.985-5.010	4.977-5.019	4.997-5.014	4.971-5.019	5.000-5.024
4.956-4.984				

4.827-4.831	5.034-5.037	4.939-4.947	5.059-5.109	4.958-4.975
4.977-5.008	4.922-4.952	5.036-5.043	4.990-5.035	5.007-5.032
4.959-4.996	4.966-4.977	4.997-5.016	4.999-5.034	4.994-5.019
5.007-5.031	4.996-5.014	5.001-5.014	4.981-5.006	4.985-5.012
4.948-5.010				

4.802-4.855	4.997-5.013	4.929-4.935	5.049-5.108	4.933-5.010
4.948-4.994	4.942-4.953	5.004-5.031	5.003-5.032	4.999-5.057
4.968-5.002	4.969-4.991	5.008-5.056	4.985-5.020	4.968-4.993
4.980-5.001	4.964-4.984	5.005-5.047	5.018-5.032	4.986-5.004
4.961-5.016				

4.840-4.893	4.997-5.003	4.891-4.931	5.066-5.077	4.935-5.018
4.978-4.995	4.936-4.966	4.966-5.010	4.971-5.018	5.025-5.044
4.961-5.001	4.958-5.010	4.999-5.010	4.972-5.061	4.962-4.975

4.951-5.015 4.974-4.997 4.966-5.028 4.973-4.993 4.935-5.010
4.929-5.005

4.837-4.893 4.984-5.000 4.913-4.925 5.071-5.083 4.916-4.986
4.967-4.975 4.926-4.937 5.002-5.006 5.004-5.008 5.009-5.031
4.991-5.026 4.989-4.997 5.008-5.014 4.985-5.017 4.985-5.025
4.953-5.042 4.999-5.014 4.993-5.021 4.994-5.011 4.975-5.013
4.999-5.019

4.845 4.993 4.944 5.035 4.957 4.969 4.968 5.029 4.976 5.018
4.996 5.012 4.989 4.985 4.960 5.037 5.042 4.973 4.976 5.020
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4.962 5.016 4.973 4.959 5.069 5.031 4.996 4.948 5.048 4.996

5.046

4.954 5.027 5.029 4.978 5.051 5.039 5.038 5.109 5.008 5.112
4.891 5.039 4.955 5.051 5.050 5.029 5.057 4.882 4.975 4.969
5.030

4.883-4.947 4.988-5.071 4.901-5.032 4.960-5.111 4.991-5.073
4.948-5.019 4.999-5.017 4.956-5.018 5.014-5.031 5.015-5.114
4.973-5.076 5.020-5.022 4.958-5.031 4.978-5.098 4.923-5.032
5.004-5.030 4.988-5.009 4.926-4.979 4.986-4.987 4.989-4.990
5.031-5.080

4.858-4.919 5.018-5.018 4.886-4.949 5.037-5.154 4.937-5.058
5.008-5.016 4.976-5.016 4.914-5.111 4.928-4.959 5.014-5.095
4.953-5.063 5.014-5.078 5.003-5.045 5.006-5.006 4.966-5.027
4.979-4.981 4.991-5.015 4.930-4.974 4.963-5.041 5.016-5.029
4.996-5.050

4.818 5.037 4.968 5.132 5.027 5.016 5.022 4.981 4.842 4.957
4.973 5.083 4.991 4.907 4.994 4.972 5.022 4.990 4.983 4.949
5.010

4.795 5.006 4.924 5.146 5.036 4.960 4.983 4.985 4.923 4.993
4.943 4.960 5.063 5.008 4.999 4.915 4.956 5.019 4.945 5.030
5.005

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5.250-5.306 4.990-5.073 4.869-5.002 4.971-5.045 4.988-5.094
4.974-5.065 4.963-5.024 5.005-5.031 5.012-5.033 5.022-5.060
5.013-5.030 4.924-5.051 4.956-4.963 4.964-4.965 4.971-5.011
4.963-5.005 5.006-5.042 5.006-5.011 4.972-4.990 4.959-4.987
4.992-4.993

5.122-5.326	4.838-4.845	4.995-5.014	5.074-5.096	5.045-5.059
5.033-5.075	4.949-4.969	5.007-5.026	4.989-5.059	5.022-5.026
4.968-4.985	4.976-5.046	4.948-4.998	4.972-4.979	4.976-4.992
5.008-5.028	4.998-5.000	4.995-5.041	5.019-5.023	5.011-5.016
4.942-5.023				

5.150-5.163	4.809-5.132	4.955-5.189	4.990-5.069	4.843-5.077
4.925-4.943	5.013-5.065	5.059-5.077	4.964-5.065	4.959-5.049
4.964-4.972	4.940-5.041	4.973-5.035	4.971-5.005	4.979-5.050
4.952-4.980	4.956-4.962	5.048-5.051	4.978-5.000	4.986-5.064
5.023-5.026				

5.114-5.139	4.874-5.071	4.954-5.059	4.932-4.956	5.020-5.108
4.927-4.984	5.012-5.053	4.958-4.995	4.918-5.042	5.028-5.097
5.017-5.077	4.978-4.990	4.983-5.062	4.956-5.044	4.977-4.995
5.011-5.031	4.985-5.024	4.949-4.995	5.008-5.020	4.981-5.033
4.993-5.025				

5.049-5.098	5.011-5.059	4.990-5.082	5.002-5.042	4.986-5.023
4.975-5.025	4.973-5.007	5.012-5.029	5.008-5.058	4.997-5.055
4.983-5.001	4.979-5.007	4.973-5.011	4.972-4.976	4.994-5.019
4.987-5.023	5.003-5.017	4.989-5.017	4.978-5.007	4.990-5.010
4.990-5.013				

5.026-5.058	4.965-5.075	4.888-4.964	4.962-4.985	4.989-5.023
5.047-5.075	4.957-4.999	4.957-5.016	4.943-4.995	5.002-5.039
4.974-5.042	4.963-5.000	4.958-5.021	4.938-4.986	4.961-4.996
4.964-4.999	4.991-5.025	4.984-5.034	4.959-4.995	5.011-5.022
4.998-5.028				

5.014-5.054	4.971-5.042	4.893-4.961	4.952-4.997	4.975-5.026
4.989-5.063	4.978-5.021	4.975-5.012	4.982-5.063	4.998-5.029
4.989-5.013	5.005-5.025	4.982-5.001	4.960-4.985	4.999-5.033
4.995-5.027	4.987-5.013	4.972-5.019	4.969-5.010	4.972-4.996
5.007-5.024				

4.972-5.006	4.996-5.050	4.925-4.973	4.961-5.003	4.983-5.026
5.010-5.030	4.963-4.993	4.970-4.979	4.978-5.038	4.974-4.993
4.988-5.019	5.002-5.032	4.965-4.989	4.965-4.991	4.990-5.030
5.006-5.045	4.969-5.004	4.976-5.008	4.978-5.022	4.997-5.029
4.985-5.021				

4.924-4.956	4.968-4.989	4.917-4.991	4.909-4.936	4.970-5.007
4.967-5.044	4.989-5.067	4.995-5.045	4.976-5.020	5.004-5.041
5.023-5.090	4.997-5.020	4.982-5.002	4.955-5.022	4.984-5.008

4.995-5.055	4.967-4.998	5.010-5.046	4.974-5.036	5.000-5.037
4.972-4.991				
4.897-4.930	4.943-5.039	4.958-4.966	4.896-4.942	4.930-4.982
4.940-4.997	4.962-5.002	5.015-5.021	4.982-4.990	5.008-5.040
4.997-5.075	4.983-5.005	4.999-5.061	5.002-5.053	4.948-5.011
4.994-5.007	4.978-4.985	5.005-5.027	5.005-5.020	5.000-5.035
4.994-5.024				
4.882-4.931	4.936-5.022	4.912-5.011	4.932-4.985	4.988-5.060
4.939-4.996	4.959-5.019	4.996-5.021	4.971-4.994	4.940-4.998
5.010-5.062	4.973-4.979	5.007-5.051	4.972-5.015	4.999-5.018
4.983-5.062	4.963-5.032	5.010-5.043	4.976-5.020	4.963-5.006
4.972-4.987				
4.882-4.915	4.961-4.990	4.911-4.963	4.953-4.994	5.002-5.015
4.945-4.966	4.977-5.026	4.937-4.979	5.032-5.070	5.009-5.049
5.037-5.044	4.933-4.976	5.010-5.026	4.977-4.993	4.956-4.978
4.980-5.034	5.006-5.026	4.954-4.965	4.994-5.034	4.977-5.027
5.003-5.053				
4.880-4.919	4.961-5.015	4.918-4.938	4.968-5.008	4.986-5.006
4.952-4.979	4.990-5.031	4.968-4.977	4.986-4.992	5.042-5.061
5.000-5.059	4.973-5.011	4.985-5.011	4.979-4.995	4.998-5.012
5.000-5.038	4.996-5.029	4.993-4.996	4.989-5.010	4.971-5.005
5.003-5.021				
4.856-4.894	4.950-4.979	4.919-4.973	4.996-5.007	4.997-5.005
4.975-4.999	5.014-5.065	4.939-4.973	4.984-5.003	5.032-5.114
4.983-5.029	5.004-5.024	4.962-4.988	4.988-5.023	5.016-5.026
5.017-5.036	5.025-5.030	4.970-4.975	4.993-5.013	5.022-5.032
4.989-5.035				
4.811-4.925	4.971-4.975	4.931-4.994	4.991-5.012	4.975-4.983
4.951-5.007	4.999-5.012	4.947-5.016	5.012-5.022	5.018-5.028
4.997-5.009	4.966-5.046	4.960-4.990	4.998-4.998	4.996-4.999
4.984-4.984	4.978-5.018	4.980-4.993	4.990-5.014	4.973-4.973
4.999-5.017				
4.818-5.071	4.991-5.003	4.840-4.952	4.998-5.096	5.004-5.030
4.942-5.021	4.955-5.003	5.012-5.028	4.977-5.010	5.004-5.066
4.969-4.999	5.004-5.004	5.002-5.019	4.963-5.023	4.991-5.014
4.988-5.015	5.012-5.040	4.996-4.998	5.005-5.019	5.005-5.006
4.981-5.001				

4.885 4.953 4.942 4.981 5.005 4.985 4.974 4.977 5.032 5.060
4.992 5.034 5.017 4.979 4.979 4.997 4.987 4.971 5.010 5.011
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5.313-5.360 4.957-5.015 4.889-4.971 4.977-4.993 5.026-5.092
5.014-5.072 4.965-5.047 5.015-5.027 4.988-5.009 5.009-5.034
4.984-5.005 5.015-5.057 4.986-5.013 4.969-4.996 4.976-4.994
5.016-5.048 4.970-4.985 4.996-5.017 5.014-5.032 4.982-4.999
4.999-5.010

5.256-5.292 4.925-5.052 4.973-5.078 4.994-5.043 5.007-5.084
4.935-5.007 4.963-5.016 4.981-5.032 4.993-5.017 4.974-5.003
4.972-5.033 4.986-5.047 4.998-5.041 5.002-5.027 4.985-5.014
4.973-4.999 4.996-5.010 4.984-5.008 4.984-5.005 4.995-5.006
4.996-5.005

5.197-5.244 4.946-5.126 5.001-5.118 4.964-4.995 4.987-5.067
4.918-4.949 4.960-5.036 5.018-5.062 4.951-4.978 4.978-5.020
4.953-4.989 4.997-5.043 4.987-5.013 5.000-5.030 4.990-5.033
4.966-5.015 4.970-4.992 4.997-5.020 4.978-4.992 5.012-5.020
4.987-5.014

5.103-5.155 4.894-5.101 4.963-5.094 4.935-4.998 4.933-5.007
4.922-4.956 5.011-5.070 5.001-5.023 4.933-4.998 4.980-5.025
4.965-5.012 4.979-5.032 4.971-5.016 4.955-4.995 4.976-5.032
4.982-5.027 4.990-5.022 4.994-5.012 5.001-5.011 4.991-5.033
4.983-4.998

5.028-5.082 4.826-5.043 5.019-5.143 4.981-5.033 4.986-5.048
4.896-4.953 4.971-5.020 4.968-5.066 4.946-5.005 4.980-5.036
4.995-5.030 5.003-5.010 4.967-5.014 4.992-5.013 5.003-5.040
4.967-5.023 4.981-5.018 5.001-5.027 5.011-5.034 4.990-5.011
4.989-5.005

4.985-5.085	4.829-5.014	5.114-5.203	4.958-5.008	4.985-4.999
4.838-4.939	4.958-5.090	4.949-4.972	4.995-5.043	5.027-5.109
4.971-5.018	5.023-5.062	4.965-5.046	5.014-5.057	4.989-5.007
4.949-4.990	5.002-5.008	4.973-5.020	5.007-5.018	4.977-5.021
4.978-5.008				

4.941-5.058	4.819-5.023	5.073-5.165	4.930-4.975	4.935-5.070
4.920-5.048	4.931-5.014	4.889-4.961	4.924-5.002	4.994-5.061
4.968-5.016	4.999-5.029	4.976-5.023	4.986-5.010	4.943-5.041
4.958-4.977	4.999-5.040	4.993-5.043	4.994-5.023	5.000-5.037
4.982-5.040				

4.878-4.928	4.933-5.013	5.140-5.238	4.969-5.023	4.931-4.977
5.024-5.071	5.014-5.066	4.989-5.023	4.935-4.968	5.003-5.050
5.025-5.058	4.992-5.033	4.955-5.003	5.051-5.060	4.978-5.019
4.953-5.010	4.964-5.008	4.972-5.043	4.971-5.019	4.971-5.005
4.972-5.002				

4.910-4.982	5.078-5.197	5.045-5.125	4.978-5.054	4.963-5.007
4.955-4.998	5.049-5.122	4.998-5.011	4.990-5.014	5.038-5.118
4.944-5.012	5.006-5.045	4.921-5.045	5.016-5.039	5.009-5.068
4.979-5.014	4.953-5.007	4.976-5.030	5.006-5.051	4.949-4.989
4.976-5.058				

4.927-5.066	5.034-5.164	4.938-5.025	4.726-4.999	4.829-5.040
4.950-5.018	4.960-5.034	5.029-5.040	4.949-4.967	5.001-5.024
4.994-5.042	4.966-5.012	4.923-4.989	4.980-5.041	4.993-5.014
4.997-5.052	4.961-5.000	4.987-5.028	4.932-4.996	4.997-5.017
5.001-5.041				

4.885-5.014	5.196-5.231	4.925-4.940	4.873-4.982	5.008-5.144
4.960-5.015	5.042-5.073	4.985-5.074	4.975-5.061	5.014-5.020
4.950-4.965	4.954-5.045	4.934-4.957	4.999-5.076	4.975-5.033
4.995-5.022	4.989-5.010	4.966-4.981	4.981-5.066	4.990-5.014
4.947-4.973				

4.910-5.033	5.099-5.249	4.798-4.900	4.951-4.970	5.129-5.137
4.921-4.932	4.985-5.023	5.019-5.083	4.956-5.075	4.937-5.001
4.894-5.018	4.929-4.994	4.949-4.990	4.981-5.053	4.960-4.983
4.942-5.070	4.972-5.060	5.005-5.021	4.975-4.977	4.990-4.994
5.001-5.034				

4.997-5.012	5.034-5.118	4.753-4.923	4.929-5.023	5.083-5.159
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4.940-5.036 4.945-5.016 5.005-5.024 4.979-5.029 4.983-5.003
4.986-5.035

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